Frisch, Ashley J. (2007) ***Population biology and fishery ecology of the painted crayfish, Panulirus versicolor, on the Great Barrier Reef*****. PhD Thesis, James Cook University.**

Population biology and fishery ecology of the painted crayfish, *Panulirus versicolor*, on the Great Barrier Reef

PhD thesis submitted by

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in September 2007

For the degree of Doctor of Philosophy

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I concieved, designed, performed, analysed and reported all sections of this thesis and associated publications. Mr Jean-Paul Hobbs, a fellow post-graduate student, assisted with the collection of data, provision of funds, and editing of text (Chapters 2 and 3 only). Dr Mark McCormick, my supervisor, provided general guidance with respect to statistical analysis and thesis writing (Chapters 1−8).

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DECLARATION ON ETHICS

The research presented and reported in this thesis was conducted within the guidelines for research ethics outlined in the *National Statement on Ethics Conduct in Research Involving Human (*1999*),* the *Joint NHMRC/AVCC Statement and Guidelines on Research Practice* (1997)*,* the *James Cook University Policy on Experimentation Ethics*. *Standard Practices and Guidelines* (2001), and the *James Cook University Statement and Guidelines on Research Practice* (2001). The proposed research methodology received clearance from the James Cook University Experimentation Ethics Review Committee (approval number A927), the Great Barrier Reef Marine Park Authority (permit number G04/12708.1), and the Department of Primary Industries (permit number PRM05020B).

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ACKNOWLEDGEMENTS

I am very grateful for the help and support provided by numerous individuals and organizations, particularly:

- Ruth Mallinson (my grandmother) for encouragement and financial support
- Sharyn Frisch and John Frisch (my parents) for encouragement, financial support, and editing of the manuscript
- Dr Mark McCormick (my supervisor) for insightful ideas about experimental marine ecology, and for giving me the freedom to explore my own ideas
- Natalka Hardeman and Rachel Groom for assistance in the field
- Katie Munkres, Ron Baker, Jean-Paul Hobbs and Peter Wruck for help in all aspects of science and social life
- Rocky De Nys, Ned Pankhurst, Chaoshu Zeng and Mike Kingsford for academic support
- James Cook University, Great Barrier Reef Marine Park Authority, Department of Primary Industries and Fisheries, Linnean Society of New South Wales, PADI Foundation and Project AWARE for provision of research funds
- James Cook University for provision of a Postgraduate Research Scholarship

This project would not have been possible without their help.

I dedicate this thesis to Mally and Danny for bringing so much fun and friendship into my life. Memories float on every tide.

ABSTRACT

Panulirus versicolor, otherwise known as the painted crayfish, is a palinurid (spiny lobster) that inhabits coral reefs of the Indo-Pacific region, including Australia's Great Barrier Reef (GBR) where it forms an esteemed component of the local recreational spearfishery. At present, management strategies for *P. versicolor* are based solely on precautionary principles, since prior to this study virtually nothing was known about this species. The broad goal of this thesis was therefore to describe the population biology and fishery ecology of *P. versicolor* on the GBR, thereby providing a framework for the development of a comprehensive management scheme for this important fishery resource.

To quantify the fishery for *P. versicolor*, teams of spearfishers conducted 135 hr of recreational fishing activities during 12 trips spread across 15 months and seven reefs. It was found that *P. versicolor* was the second most abundant component of the catch, after common coral trout (*Plectropomus leopardus*). Catch per unit effort (CPUE) was estimated to be 0.155 ± 0.025 crayfish hr^{-1}, which is equivalent to one crayfish for each 6.4 hr of spearfishing. Assuming this CPUE was representative of the recreational spearfishery as a whole, and given 37,110 hr as the total annual spearfishing effort on the GBR (Henry and Lyle 2003), the total annual catch of *P. versicolor* was estimated to be 5,773 ± 928 individuals (8,660 ± 1,530 kg). By world standards, this amount is relatively small. However, because this species is highly sought-after and is not abundant anywhere within its distributional range, fishing pressure on *P. versicolor* in readily accessible areas of the

GBR may still be relatively high. Thus, a comprehensive management scheme should be implemented to ensure this species is not over-exploited.

Development of a fishery management scheme requires knowledge of a range of population parameters (*e.g*. abundance, growth, mortality) which can be estimated by mark-recapture techniques. However, it was first necessary to develop a method of tracking individual crayfish in the wild, since most conventional tagging methods are ineffective due to moulting of the exoskeleton. As such, three unconventional tracking methods (ablation, elastomer implants, photographic identification) were evaluated in the field over periods of 6–36 months. Ablation proved to be ineffective due to a high incidence of infection and exoskeletal repair. In contrast, elastomer implants and photographic identification were shown to be highly effective (96.5% and 100% effectiveness, respectively), even after numerous episodes of moulting. Consequently, only the latter two methods were used for the remainder of the study.

To investigate the population biology of *P. versicolor*, a multiple mark-recapture program was conducted at Northwest Island, an offshore coral cay in the GBR complex. Censuses were performed daily for ten consecutive days on six occasions between December 2003 and December 2006, thereby enabling estimation of population parameters over both short- (1−10 d) and long-term (6−36 months) periods. Fifty-six percent of crayfish (50/89) were recaptured (resighted) after 1−10 d, whereas 59% of crayfish (50/85) were recaptured after 6−36 months. Some animals were recaptured (or resighted) on multiple occasions; hence, there were 122 short-term observations and 86 long-term observations.

Ovigerous female crayfish were captured in both summer and winter, suggesting that this species has a protracted spawning period. Although some females reproduced *in situ*, the majority of mature females appeared to emigrate temporarily during summer, resulting in a male-biased local population at that time. Using a sample of crayfish from both inshore and offshore reefs, the size at first maturity (SFM) was estimated to be 88 and 78 mm carapace length (CL) for males and females, respectively. This is substantially larger than estimates of SFM for *P. versicolor* from Western Australia, which may reflect regional differences in either environmental conditions or fishing pressure.

Growth of *P. versicolor* was shown to be asymptotic and well described by a von Bertalanffy growth model (L_∞ = 144.7 mm CL; K = 0.27 yr^{-1}; t_0 = -0.18 yr). Moult interval for larger (>125 mm CL) and smaller (90−125 mm CL) individuals was estimated to be 326 ± 31 and 159 ± 18 d, respectively. Growth increment was estimated to be 2−3 mm CL and appeared to be constant across the range of sizes examined (98−153 mm CL). In general, growth of *P. versicolor* was similar to that of other tropical palinurids, but markedly faster than that of temperate palinurids, which supports the notion of increasing growth rate with decreasing latitude.

The population of *P. versicolor* at Northwest Island was estimated to be small in size (1,400 ± 185 individuals) and sparsely distributed (1.3 ± 0.2 individuals ha^{-1}). The estimated total mortality rate (0.28 ± 0.04 yr^{-1}) was low and probably represented only natural mortality, because the study was conducted at a relatively inaccessible part of the reef that was rarely or never fished. With respect to replenishment of the population, preliminary observations suggested that individuals recruit to inshore reefs and then

migrate offshore as they approach maturity – an ontogenetic pattern that is characteristic of palinurids in general.

Adult crayfish were found to aggregate in dens during the day. At night, individuals moved to and from nearby dens, such that group composition changed frequently. Despite this, two male crayfish never occupied the same den simultaneously, indicating that groups were not merely random mixtures of individuals. Surprisingly, the relationship between body size (CL) and male social status (number of co-habiting females) was weak or non-existent, and experimental translocation of single male and female crayfish to occupied dens did not result in eviction, regardless of CL. Thus, body size appears to be less important in shaping the social system of *P. versicolor* than it is in other species.

Despite the capacity to move considerable distances during short periods of time (*i.e.* up to 459 m d^{-1}), at least 59% of tagged individuals (50/85) remained within a 60 ha reef area for at least 6−36 months. Also, these individuals were shown to repeatedly inhabit the same, readily identifiable dens. That *P. versicolor* lives in predictable places and maintains a high level of site-fidelity predisposes this species to over-exploitation, which underscores the need to implement effective management strategies.

Based on the results of this study and assuming the presence of a large unfished breeding population, three important management desiderata were identified. Firstly, the current prohibition on possession of spermatophoric and ovigerous females should be revoked. This will reduce wastage of breeding females that are currently inadvertently killed by the fishery. The basis of this recommendation is that there appears to be little chance of localised recruitment overfishing and hence there is little need to protect breeding females at a local level. Secondly, introduction of a 100 mm CL minimum size limit would optimise yield and population biomass without greatly impacting current fishing practices. Thirdly, establishment of small marine reserves (1−2 km in dimension) is an effective strategy to counteract localised depletion of adult *P. versicolor*, since individuals appear not to roam widely. Implementation of these knowledge-based management strategies will help to ensure this highly desirable fishery resource is exploited on a sustainable and rational basis.

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CHAPTER 1: General Introduction

1.1 The Palinuridae

The Palinuridae, otherwise known as spiny lobsters, are a group of 47 decapod crustaceans that are united by two distinct morphological features: the absence of chelae (or claws) and the presence of many sharp spines on the carapace and antennae (Holthius 1991). The basic body plan otherwise resembles that of their clawed cousins, the Nephropidae: both have a carapace, six abdominal somites, 4−5 pairs of walking legs, and two pairs of antennae (Phillips *et al*. 1980). The maximum body size of most palinurids is in the order of 3−5 kg, although some species grow to 10 kg or more, which ranks them among the largest of all crustaceans (Lipcius and Eggleston 2000).

Palinurids are ubiquitous in tropical and temperate seas around the world and generally inhabit rocky or coral reefs in shallow water (Lipcius and Eggleston 2000). Population densities are typically in the order of 50−500 individuals ha^{-1} (Forcucci *et al*. 1994; Dennis *et al*. 1997; Sharp *et al*. 1997), although values as high as 2000 individuals ha^{-1} have been recorded in some habitats (Morgan 1974). Despite their abundance, individuals tend to be inconspicuous, at least to casual human observers. This is because palinurids normally occupy protective coral or rock shelters known as dens. Only at night do they emerge to forage across the shallows for benthos (Butler *et al*. 2006).

The lifecycle of all palinurids is complex – a benthic adult phases is preceded by a planktonic larval phase (phyllosoma) which, in tropical species, typically lasts 4–8 months

(Dennis *et al*. 2001; Phillips *et al*. 2006). Settlement of postlarvae (pueruli) usually occurs in shallow, inshore areas such as rocky reefs and seagrass beds, and the developing juveniles normally remain in these habitats for the first 1–2 yr of life (Butler and Herrnkind 2000; Butler *et al*. 2006). As individuals approach adulthood they tend to migrate offshore, at which time they also undergo changes in social behaviour. Whereas early juvenile stages are predominantly asocial, adults are facultatively gregarious; groups of 100 or more can be found sheltering in dens or migrating in long queues across the seafloor (Kanciruk 1980). The adaptive value of this social behaviour is thought to be enhanced protection from predators such as sharks and fish (Herrnkind *et al*. 2001; Butler *et al*. 2006).

Throughout life, palinurids are opportunistic foragers and consume the same types of prey: molluscs, crustaceans, echinoderms and algae (see Butler *et al*. 2006 and references therein). Due to their large size and often great local abundances, palinurids are capable of altering the benthic community in which they live, either *via* direct effects on prey species or *via* cascading effects involving both competitors and prey (Tegner and Dayton 1981, Andrew and MacDiarmid 1991). Thus, palinurids are ecologically consequential organisms – a notion that highlights our need to better understand and effectively manage this important group of animals (Lipcius and Eggleston 2000; Butler *et al*. 2006).

1.2 Palinurid fisheries and management

Palinurids are a highly esteemed seafood, not just in places where they are captured, but all over the world. At restaurants in Japan and Hong Kong (the two largest importing countries), diners are willing to pay more than AU \$120 kg^{-1} (Phillips and Kittaka 2000). Consequently, spiny lobsters are a high-value commodity, and commercial fisheries have developed wherever these animals are found in high abundance (Pitcher 1993). At present, the major exporting countries are Australia, New Zealand, South Africa, Cuba, Brazil and U.S.A. The dominant species are *Panulirus argus*, *Panulirus cygnus* and *Jasus edwardsii*, which together comprise about 70% of the total world catch (Lipcius and Eggleston 2000). In the year 2000, the global catch was estimated to be 77,000 metric tonnes, with a landed value of approximately US \$500 million (Phillips and Kittaka 2000).

Due to the increasing size and wealth of the human population, the future demand for spiny lobsters is expected to increase. However, all of the world's major commercial fisheries for spiny lobsters are now considered to be either fully exploited or over-exploited (Phillips and Melville-Smith 2006). The need for effective management of existing spiny lobster populations is therefore critical.

In general terms, the objective of fishery management is to maximise economic and social benefits by allowing exploitation of a stock whilst maintaining its reproductive capacity at a high level (King 1995; Walters and Martell 2004). Common management strategies used for spiny lobster fisheries include gear restrictions, size limits, catch limits, and closed seasons (Annala and Sullivan 1997). In recent decades, marine reserves have become very popular, although considerable debate exists as to their appropriate design (*e.g.* many small *versus* few large) (Butler *et al.* 2006). Although the effectiveness of different strategies varies world-wide, it is clear that spiny lobster fisheries that are intensively managed (*e.g.*

P. cygnus in western Australia) perform better and outlast those that are minimally managed (*e.g. Panulirus polyphagus* in India) (Phillips and Melville-Smith 2006).

For any fishery, it is best if management decisions are based on rigorous scientific research. This usually involves acquiring knowledge about both the fishery (*e.g*. catch per unit effort) and the biology of the animal (*e.g*. size at first maturity; SFM). Due to the enormous value of *P. argus*, *P. cygnus* and *J. edwardsii* to commercial fisheries, most of our current knowledge of palinurid biology has come from studies of these few species (Cobb and Phillips 1980; Phillips 2006). Much less is known about other species, especially those that support only artisanal or recreational fisheries. One consequence of this knowledge gap is that the lesser-known species may be more vulnerable to over-exploitation.

1.3 Palinurids in the tropical west Pacific

Four species of palinurids support artisanal and recreational fisheries in the tropical west Pacific. These are *Panulirus penicillatus*, *Panulirus ornatus*, *Panulirus longipes* and *Panulirus versicolor* (Dalzell *et al*. 1996; Munro 2000). Although all four have distributions that overlap extensively, they are not generally found together, since each has slightly different ecological preferences. For example, *P. ornatus* is typically found in rocky or silty areas on continental shelves, whilst *P. penicillatus* is more common on the windward slopes of coral reefs where wave energy is high (George 1974).

Two features of palinurids from the tropical west Pacific are of particular interest. Firstly, local abundance is generally low, much lower than for their temperate counterparts (Pitcher 1993; Munro 2000). Consequently, palinurids in the region tend not to be fished commercially, the only major exception being the fishery for *P. ornatus* in Torres Strait (between Australia and Papua New Guinea). Secondly, this group of spiny lobsters is reluctant to enter traps and pots – the standard commercial fishing gear for all temperate species (Munro 2000). Hence, fishers in the tropical Pacific must use spears, hand-nets, or their hands (Dalzell *et al*. 1996).

In global terms, the harvest of spiny lobsters in the tropical west Pacific is very small (<10,000 t yr^{-1}) (Pitcher 1993; Munro 2000). Due to low local abundance, however, fishing pressure on palinurids in this region may be very high. For example, estimates of instantaneous fishing mortality (*F*) for *P. penicillatus* in Tonga and Samoa range from 0.3 to 1.3 yr^{-1} (Pitcher 1993), whereas estimates of *F* for 'fully-exploited' *P. argus* in the Florida Keys (U.S.A.) range from 0.2 to 0.9 (Muller *et al*. 1997). It is therefore very worrying that no well founded management scheme is in place for any stock in the entire tropical west Pacific region, apart from *P. ornatus* in Torres Strait (Munro 2000).

1.4 The painted crayfish, *Panulirus versicolor*

The most common species of palinurid on the Great Barrier Reef (GBR), Australia, is *Panulirus versicolor* (Latreille), otherwise known as painted crayfish, painted lobster or coral lobster (Jones and Morgan 1994). In this thesis, the term painted crayfish is used, since this is vernacular in the local area (Queensland, Australia).

Painted crayfish are morphologically similar to most other palinurids, except that their colouring is highly ornate. The carapace and abdomen are green with black reticulation, and the bases of the antennae are bright pink (Figure 1.1). Although painted crayfish are distributed widely (Indo-West Pacific; Phillips and Melville-Smith 2006), individuals prefer shallow reef lagoons with high coral cover (George 1968, 1974). The GBR is no exception: modest numbers of painted crayfish can be found wherever this type of habitat exists (Author's personal observation).

Figure 1.1 A solitary painted crayfish (*Panulirus versicolor*) seeking shelter in its den.

Queensland is home to some 800,000 recreational fishers, many of whom make regular catches of painted crayfish on the GBR (Cadwallader *et al*. 2000; Williams 2002; Henry and Lyle 2003). Despite this, the biology and fishery characteristics of this important resource are virtually unknown. In fact, only two previous studies have addressed any aspect of this species, anywhere in the world. George and Morgan (1979) collected animals from Western Australia and estimated that SFM of males and females was 72 and 65 mm carapace length (CL), respectively. MacDonald (1982) collected animals from Palau (Micronesia) and estimated that SFM of females was 82 mm CL. He also found that reproductive activity among local stocks was sustained throughout the year. Although these results are useful as a guide, their applicability to painted crayfish on the GBR cannot be assumed. This is because biological characteristics often vary substantially among populations of the same species (McGarvey *et al*. 1999; Phillips *et al*. 2000).

At present, management strategies for painted crayfish on the GBR are based solely on precautionary principles rather than quantitatively-derived population parameters, since these are yet to be determined. As such, current management regulations are limited to (1) a catch limit of five *P. versicolor* per person (or 10 per boat), and (2) a prohibition on possessing females in ‘mated’ (spermatophoric) or ‘ovigerous’ (egg-bearing) condition (see Chapter 4 for definitions of reproductive stages). Numerous small ‘no take’ marine reserves have also been established with the general aim of conserving biodiversity (Fernandes *et al*. 2005), but their effectiveness for protecting highly mobile palinurids remains unknown. For these reasons, as well as the low abundance and high value of *P. versicolor*, the conservation status of this species is precarious.

To implement a comprehensive management scheme for *P. versicolor*, a considerable amount of biological and fishery-related information is required (*e.g*. total catch, SFM, reproductive seasonality, growth, mortality, movement patterns). Unfortunately, *P. versicolor* presents three particular challenges that make acquisition of this information very difficult. Firstly, gathering recreational catch data is hindered by the lack of reporting requirements for recreational fishers and the dispersed nature of their landings along the coast. Secondly, it is difficult to collect specimens for study because of low local abundance – a situation that generally results in small sample size and low statistical power. Thirdly, and perhaps most importantly, it is very difficult to track these animals through time and space due to tag-loss during moulting of the exoskeleton (Stonehouse 1978; Frisch and Hobbs 2006, 2007). These problems must be resolved to enable estimation of important biological and fishery-related parameters for this species. Only then can a comprehensive management scheme for *P. versicolor* be designed and implemented.

1.5 Project aims

The broad goal of this thesis was to estimate important biological and fishery-related parameters for *P. versicolor* on the GBR, thereby providing a framework for the development of a comprehensive management scheme for this important fishery resource. To achieve this goal, a number of specific aims were addressed:

- to estimate total catch (and catch rates) of painted crayfish in the GBR recreational spearfishery (Chapter 2)
- to evaluate different methods of tracking painted crayfish in the wild (Chapter 3)

- to estimate important population parameters of painted crayfish such as growth, reproduction (Chapter 4), size structure, abundance, mortality (Chapter 5) and movement patterns (Chapter 6).

Lastly, because of the complex social behaviours shown by palinurids (Atema and Cobb 1980; Segura-Garcia *et al*. 2004), an attempt was made to describe the mechanisms that govern social organisation and den utilisation of this species (Chapter 7).

For logistical reasons, much of the data were collected from one location, Northwest Island, which is an offshore coral cay in the GBR complex (Figure 1.2). Whilst it would have been ideal to collect data from a range of different locations, Northwest Island was the only place known to the author where modest quantities of painted crayfish could be captured relatively easily and reliably. The implications of this spatially-restricted sampling design are discussed in Chapter 8.

Each time a crayfish was captured (or recaptured) at Northwest Island, data relating to its size, specific location, reproductive condition, *et cetera*, were recorded. This enabled various population parameters such as growth, movement and reproductive seasonality to be investigated simultaneously using the same group of individuals. However, conscientious readers will notice different sample sizes are presented in each of the relevant chapters. This is because some types of data were not collected for some individuals (*e.g*. due to equipment malfunction) or because some individuals were excluded from some sections (*e.g*. juvenile crayfish were excluded from Chapter 7, which relates to social biology).

Most of the information contained in this thesis has been formally published (see Frisch 2005, 2007a, 2007b, 2008; Frisch and Hobbs 2006, 2007; Frisch *et al*. 2008). In some cases, the published results differ from the results presented here, because additional data were collected after the relevant manuscripts were submitted for publication. However, these differences are small and do not affect the overall conclusions.

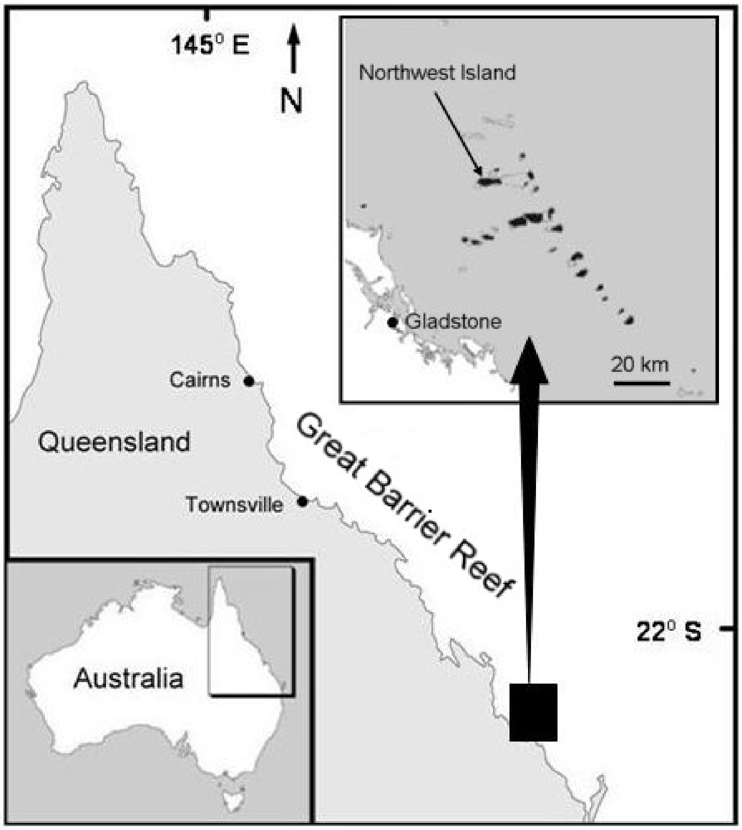

Figure 1.2 Map showing the location of Northwest Island, a coral cay in the Great Barrier Reef complex.

CHAPTER 2: Recreational harvest of painted crayfish

Abstract

Estimation of total catch and catch per unit effort (CPUE) is essential for predicting the impacts of fishing on an exploited species. However, neither of these parameters have ever been derived for painted crayfish (*Panulirus versicolor*) on the Great Barrier Reef (GBR). To address this issue, small teams of spearfishers were engaged in recreational fishing activities during discrete time intervals, thereby enabling direct estimation of CPUE. It was found that painted crayfish were the second most abundant component of the catch, after common coral trout (*Plectropomus leopardus*). Catch per unit effort was estimated to be 0.155 ± 0.025 crayfish hr^{-1}, which is equivalent to one crayfish for each 6.4 hr of spearfishing. Assuming this was representative of the entire recreational spearfishery, and given 37,110 hr as the total annual spearfishing effort on the GBR (Henry and Lyle 2003), the total annual catch of *P. versicolor* was estimated to be 5773 ± 928 individuals. It was concluded that fishing pressure on *P. versicolor* may be relatively high in readily accessible areas because this species is not abundant anywhere within its distributional range. Thus, a comprehensive management scheme should be implemented to ensure that *P. versicolor* is not over-exploited.

2.1 Introduction

The GBR is the largest coral reef in the world. It covers an area of 20,300 km^2 and extends over 15^o of latitude, which is most of the east coast of Queensland, Australia (Anon. 1990). There are over 2,100 individual reefs, each separated by distances ranging from a few hundred metres to tens of kilometres. The majority of reefs are platform reefs that lie 30−150 km offshore. The remainder are fringing reefs that grow around inshore or midshore islands. Painted crayfish can be found wherever there is extensive coral growth, either on platform or fringing reefs (Author's personal observation).

The principal method of catching painted crayfish on the GBR is spearfishing, which involves a rubber-propelled spear, as well as associated dive gear such as mask, snorkel and fins. Under Queensland law, spearfishing with the aid of SCUBA is prohibited; so too is commercial spearfishing (Anon. 1995). Recreational fishing thus accounts for 100% of the catch of painted crayfish in the GBR region. In terms of spatial distribution, virtually all spearfishing occurs on midshore or offshore reefs. This is because spearfishing is generally too difficult along the mainland coast where water visibility is greatly reduced (see Wolanski and Jones 1981). To access the preferred areas, most spearfishers operate from small (4−6 m), outboard-powered boats with 1−5 fishers per boat (Hundloe 1985).

It is estimated that 107,100 people participate in some form of recreational fishing (spearfishing, angling, gleaning, etc.) on the GBR each year (Blamey and Hundloe 1993; Williams 2002). These fishers harvest approximately four million kilograms of living reef resources (fish, molluscs, crustaceans, *etc.*) – an amount that is expected to rise rapidly with the spread of 'high-tech' fishing equipment and increasing human population size (Blamey and Hundloe 1993). Even at current levels, the potential impact of recreational fishing is likely to be substantial. This prompts the need for stringent management of exploited reef resources, particularly those that are valuable and highly sought-after.

At present, comprehensive management schemes are in place for most species that are targeted by recreational fishers (*e.g.* coral trout, *Plectropomus leopardus*) (Williams 2002). This is not the case for painted crayfish (*Panulirus versicolor*), primarily due to the lack of biological and fishery-related information about this species (see section 1.4). An important step toward resolving this deficiency is to quantify the fishery for *P. versicolor* in terms of total catch and CPUE. These statistics are vitally important inputs for assessment of the impacts of recreational fishing and for the development of appropriate management regulations (King 1995; Walters and Martell 2004).

In the absence of a catch reporting system or a centralised landing point, there are two empirical methods for estimating catch statistics of the recreational fishery. One method is to directly observe the catch of fishers who are engaged in fishing activities, while the other is to distribute questionnaires that seek information about fisher's catches during a defined period of time. Due to the enormous size of the recreational fishing population, both methods require sampling and subsequent extrapolation. However, questionnaires have one additional drawback: catch data tend to be strongly influenced by 'recall bias' (Tarrant and Manfredo 1993; Connolly and Brown 1995). For this reason, direct observation is the preferred method of estimating catch statistics.

The aim of this chapter was to quantify the recreational fishery for *P. versicolor* in terms of total catch and CPUE. To achieve this aim, small teams of spearfishers conducted recreational fishing activities during discrete time intervals, thereby enabling direct estimation of CPUE. Fishers were completely unaware of the author's particular interests in *P. versicolor* and were thus allowed to spear any of the wide range of species they would normally target. To estimate total catch, CPUE was multiplied by the total annual spearfishing effort on the GBR, which Henry and Lyle (2003) estimated to be 37,110 hr. Importantly, this estimate of total effort is considered to be accurate, since it was derived *via* a large-scale, random survey of Queensland households and was cross-validated using fisher logbooks and boat-ramp surveys.

2.2 Materials and methods

2.2.1 Field surveys

Twelve teams of two spearfishers (one spear or speargun per person) conducted recreational fishing activities aboard small (4−6 m) boats. As only one boat was available at any one time, each team operated on a different day (*i.e.* twelve separate one-day 'trips'). To standardise fishing effort among fishers and over time, all fishing was conducted in discrete 1.5 hr 'sessions' (3−4 sessions per trip, 45 sessions in total). Consecutive sessions during the same trip were separated by a short recess (0.25−1 hr) and all fishing activities were completed between 0800−1700 hrs during the period May 2005 to July 2006.

Each session of fishing was conducted at a different site that was chosen arbitrarily. Sites were spread across four offshore reefs (Bramble, Britomart, Trunk and Walker Reefs) and three midshore reefs (Palm, Barber and Curacoa Islands), all of which are located in the Townsville region of the GBR (Figure 2.1). For a complete description of the habitat, as well as estimates of the distribution and abundance of target fish species, see Done (1982) and Newman *et al*. (1997).

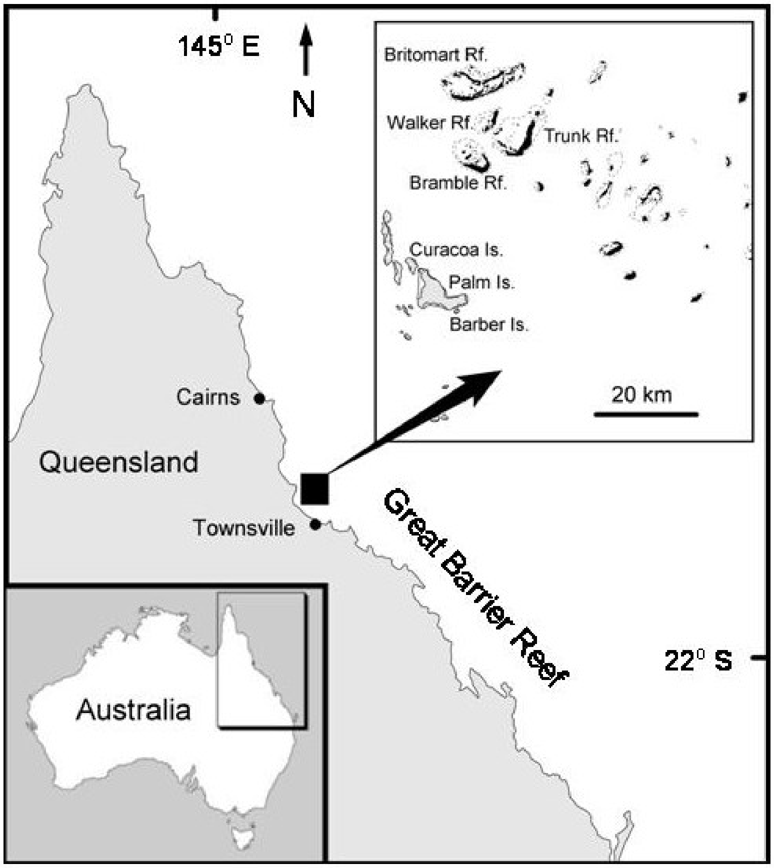

Figure 2.1 Map showing the location of spearfishing sites in the Townsville region of the Great Barrier Reef.

Given that catch rates are influenced by a fisher's skill and experience (Lincoln Smith *et al*. 1989; Mann *et al*. 1997), it was important to select fishers that were representative of the entire GBR spearfishing population. This was achieved by selecting only those people who (1) regarded themselves as competent (but not expert) spearfishers, (2) had several years of spearfishing experience, and (3) had been spearfishing within the last six months. Also, as many different fishers as could be recruited were engaged in the study. Hence, there were nine different fishers and the median number of trips per fisher was two.

2.2.2 Data collection and analysis

The identity, size, number and fate of all captured organisms were recorded shortly after capture. Where possible, captured organisms were identified to species level according to Randall *et al*. (1990) or Jones and Morgan (1994). For painted crayfish, body size was recorded as carapace length (CL), which is the distance between the sub-orbital ridge and the posterior dorsal edge of the carapace. Measurements were recorded to the nearest millimetre using a standard tape-measure. The fate of each animal was categorised as either 'retained', 'discarded' or 'escaped injured'. Animals that escaped without injury were disregarded.

To establish a length-weight relationship for painted crayfish, the weight of each animal was measured 'at sea' using a standard spring-balance (± 25 g). To improve the accuracy of the predicted relationship, the sample size was bolstered by inclusion of additional samples that were either donated by the fishing public or collected later by the author (see Chapters 4−7). These additional samples were measured 'on land' using an electronic balance (±1 g). Any animal that was missing a substantial portion of its body or appendages was excluded from the analysis. The length-weight formula was calculated by least squares regression analysis using the generalised equation:

$\text{weight} = a \times \text{CL}^b$

where a and b are unknowns, weight is expressed in kilograms, and CL is expressed in centimetres (Kulbicki *et al*. 2005).

To calculate CPUE, the number of painted crayfish captured during each session was divided by the amount of time spent fishing (1.5 hr per fisher), thus giving units of crayfish hr^{-1} (averaged across both fishers). Next, CPUE values for each trip were transformed $[\sqrt{(x + 0.5)}]$ to stabilise variances and then compared using one-way ANOVA (Zar 1999). The overall CPUE was calculated by dividing the total number of painted crayfish in the catch by the total amount of time spent fishing (135 hr).

Statistical analyses were performed using SPSS computer software (SPSS, Chicago, U.S.A.) and a significant difference was considered to exist if $p < 0.05$ (Zar 1999). All data listed in the text and figures (in this chapter and in all subsequent chapters) are the arithmetic mean (± one standard error) of untransformed data, unless otherwise stated.

2.3 Results

2.3.1 Catch composition

One hundred and thirty-five hours of spearfishing resulted in the capture of 156 organisms from 21 species (excludes organisms that escaped injured or were discarded). Common coral trout (*P. leopardus*) and painted crayfish (*P. versicolor*) were the most popular species, comprising 52% and 14% of the catch respectively. The remaining portion of the catch consisted of a variety of fishes including bar-cheek coral trout (*Plectropomus maculatus*; 6%), parrotfish (*Scarus microrhinus*; 6%), blue-spot coral trout (*Plectropomus laevis*; 4%) and flowery rockcod (*Epinephelus fuscoguttatus*; 3%) (Figure 2.2).

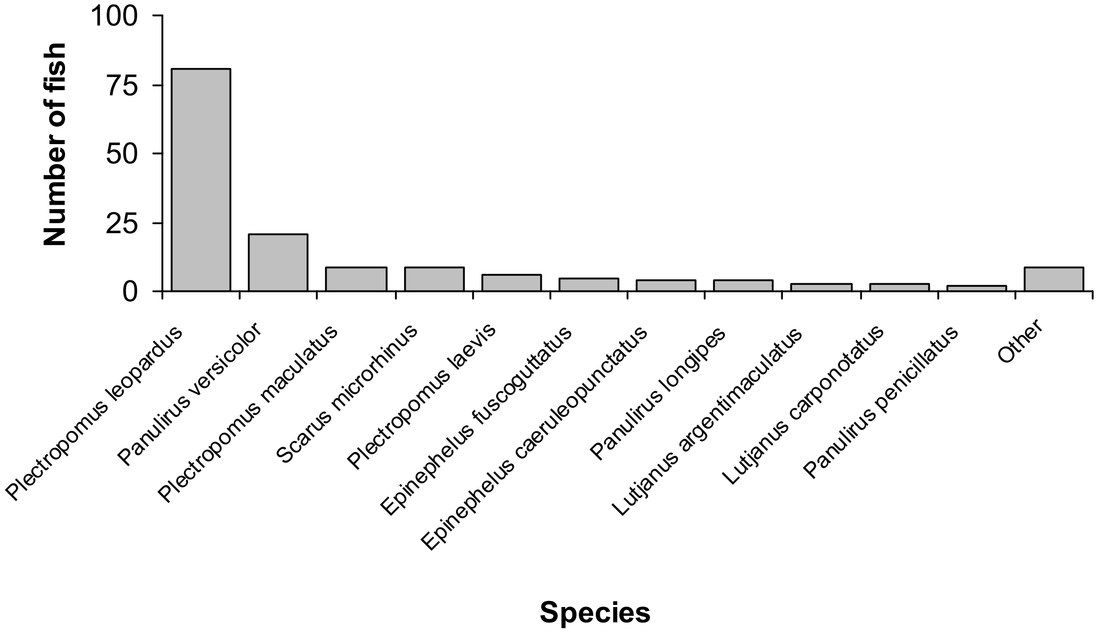

Figure 2.2 The composition of spearfishers' catch after 135 hr of recreational fishing on the Great Barrier Reef. Excludes organisms that escaped injured or were discarded.

Twenty-one *P. versicolor* were retained as part of the catch. An additional three *P. versicolor* were speared but escaped before retrieval. Whether these animals died as a result of spear-induced injuries was not known. One animal was discarded (dead) after it was found to be ovigerous, in which case it was protected by law (Anon. 1995).

In terms of body size, the mean and range of captured *P. versicolor* were 116 ± 3 mm CL and 85−142 mm CL, respectively (Figure 2.3). The weight of *P. versicolor* increased allometrically with CL (Figure 2.4). This relationship was significant (ANOVA, $F_{1,38}$ = 5638, $p < 0.001$; $r^2 = 0.99$) and was well described by the equation:

$$\text{weight (kg)} = 0.001 \times \text{CL(cm)}^{2.98}$$

Using this equation, the mean weight of painted crayfish in the catch was estimated to be 1.50 ± 0.11 kg.

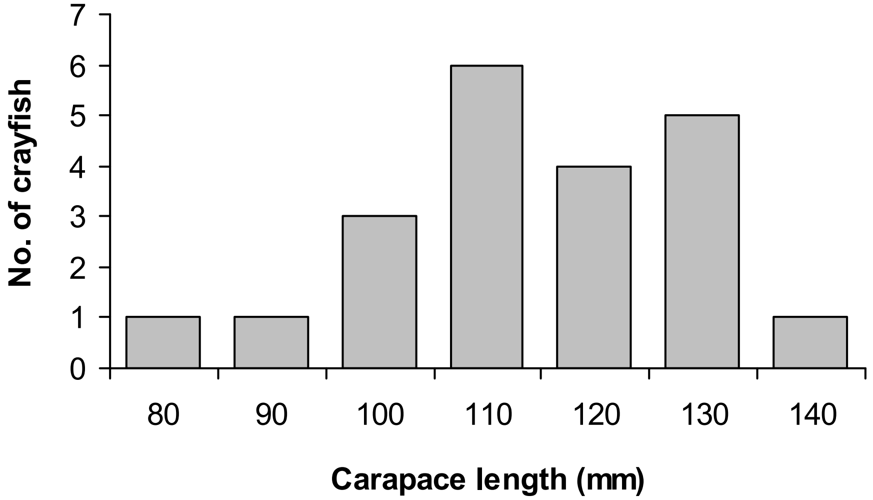

Figure 2.3 Length-frequency distribution of *Panulirus versicolor* that were captured during 135 hr of recreational spearfishing on the Great Barrier Reef. Data exclude individuals that escaped injured or were discarded. The *x*-axis labels are size-class midpoints.

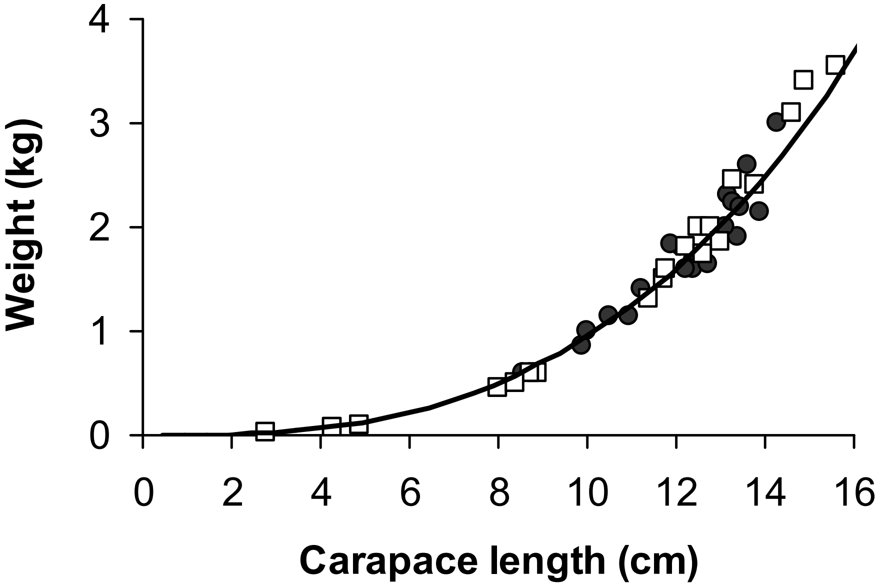

Figure 2.4 Length-weight relationship for *Panulirus versicolor* that were captured during 135 hr of recreational spearfishing (*closed circles*). Additional samples (*open squares*) were donated by the public or collected later by the author. Both groups of samples were used to calculate the regression line (weight = 0.001 × $CL^{2.98}$).

2.3.2 Catch per unit effort

For each of twelve trips, CPUE ranged from 0.08−0.25 crayfish hr^{-1}, but differences between trips were not significant (ANOVA, $F_{11,33} = 0.39$, $p = 0.95$; Figure 2.5). Given that 21 painted crayfish were captured during 135 hr of spearfishing, the overall CPUE was estimated to be 0.155 ± 0.025 crayfish hr^{-1}, which is equivalent to one crayfish for each 6.4 hr of spearfishing. Assuming this amount is representative of the entire recreational spearfishery, then the total annual catch of painted crayfish in the GBR region is estimated to be 5773 ± 928 (*i.e.* 37110 hr × 0.155 crayfish hr^{-1}). Similarly, if individuals have a mean weight of 1.50 ± 0.11 kg (see above), then the total weight of the catch is estimated to be 8660 ± 1530 kg.

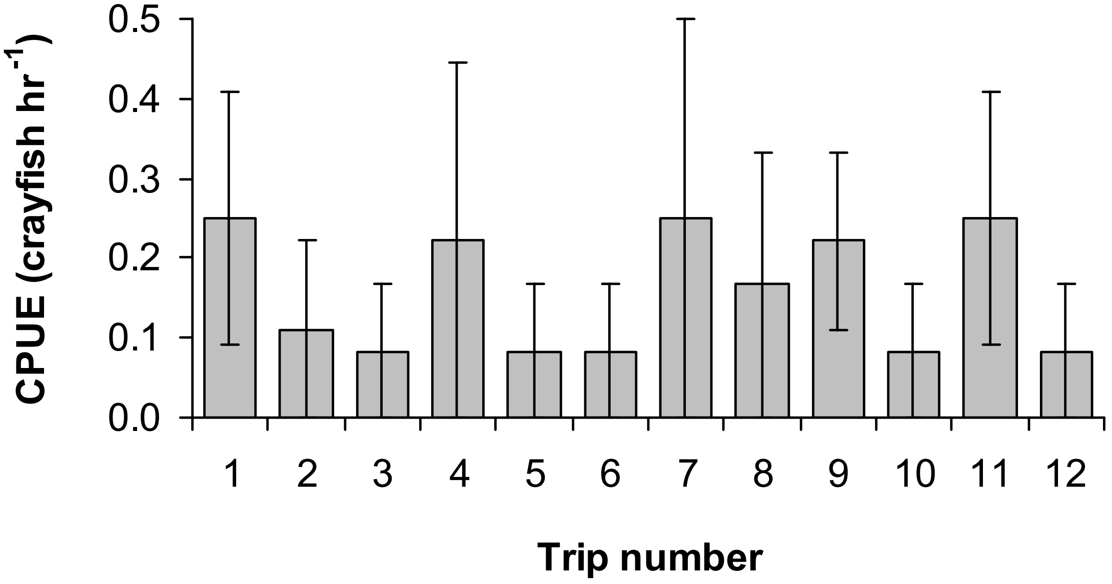

Figure 2.5 Mean catch per unit effort (CPUE) of *Panulirus versicolor* for each of twelve spearfishing trips to the Great Barrier Reef. Each trip involved two people that concurrently spearfished for four 1.5 hr sessions (three sessions in the case of trips 2, 4 and 9). Error bars (±1 SE) depict variation among sessions (within trip). Differences between trips were not statistically significant ($p = 0.95$).

2.4 Discussion

Results suggest that *P. versicolor* is an important component of the recreational spearfishery on the GBR. In fact, *P. versicolor* was the second most popular species in the catch, after *P. leopardus* (common coral trout). This result highlights the need to effectively manage stocks of *P. versicolor*, especially given the large number of recreational fishers operating in the GBR region, and the potential of this group to impact upon crayfish populations (Henry and Lyle 2003; Cooke and Cowx 2004).

The total catch of *P. versicolor* on the GBR was estimated to be 8660 ± 1530 kg. The literature on this species presents only two previous estimates of total catch anywhere in the world: Kuthalingam *et al*. (1980) found that 3794 kg of *P. versicolor* were captured annually in Vizhinjam (India), while MacDonald (1982) found that 1188 kg of *P. versicolor* were captured annually in Palau (Micronesia). Compared with other palinurid fisheries (see Phillips and Melville-Smith 2006), these quantities are very small. However, it must be remembered that the density of *P. versicolor* is relatively low throughout its distributional range (see section 1.3). For this reason, fishing pressure on *P. versicolor* may be much higher than is immediately obvious, especially in readily accessible areas.

Typically, the magnitude of a fishery is described in terms of the total number of target animals that are captured by the fishery (*i.e.* total catch). However, the proportion of animals that are discarded or incidentally injured contributes to the overall impact of a fishery and thus should be integrated into any contemporary management regime (Jennings *et al*. 2001; Parsons and Eggleston 2007). In this study, one painted crayfish was discarded (dead) and three painted crayfish escaped with spear-induced injuries. Thus, the total number of animals that died as a result of fishing may be as much as 19% higher than that indicated by the total catch. Whilst the ultimate fate of injured animals was not known, it seems likely that all of them would have died shortly after being injured. This is because palinurids have an 'open' type blood circulation and puncture of the carapace or abdomen usually results in massive haemorrhage (Phillips *et al*. 1980; Randall *et al*. 2002).

The incidental mortality of an ovigerous female raises an important management issue for the GBR fishery. Whilst it is illegal to spear ovigerous or mated females (Anon. 1995), it is virtually impossible to discern the reproductive condition of crayfish in the wild (at least in the moments just prior to releasing the spear), since both spermatophore and eggs are secluded from the diver's vision (see Figure 1.1). The law protecting mated or ovigerous females, whilst well intended, would thus seem to be wasteful in a fishery where spearfishing is the predominant method of harvest. Hence, it may be better to abolish this law and instead implement a 'closed season' when reproduction occurs (or is maximal).

The CPUE of painted crayfish on the GBR was estimated to be 0.155 ± 0.025 crayfish hr^{-1}, which is equivalent to 0.21 ± 0.03 kg hr^{-1}. Elsewhere in the tropical west Pacific region, catch rates of spiny lobsters tend to be much greater (*i.e.* 1.5−5.1 kg hr^{-1}, Dalzell *et al.* 1996). However, it must be remembered that the GBR fishery is a multispecies fishery and that participants probably direct most of their effort toward the capture of fish (*e.g.* coral trout) rather than painted crayfish (see Figure 2.2). Also, recreational fishers on the GBR are likely to be less experienced and less motivated than artisanal or subsistence fishers that operate elsewhere in the tropical west Pacific region (Ruddle 1996). Direct comparisons of CPUE between the GBR and other tropical west Pacific fisheries must therefore be treated with caution.

One potential limitation of this study was the small size of the sample (only 21 painted crayfish in 135 hr of fishing). However, CPUE was found to be relatively stable among trips (Figure 2.5), despite the fact that fishing occurred at seven different locations and involved nine different fishers. This low level of variation suggests that the parameters derived here are reasonably accurate and that additional sampling was probably not required.

In conclusion, *P. versicolor* is a highly sought-after species that may be subject to substantial fishing pressure in readily accessible areas. Thus, a comprehensive management scheme should be implemented to ensure this species is not over-exploited. Also, it seems that input controls (*e.g.* a ‘closed season’) would be more appropriate than output controls with regard to protecting spawning females, since reproductive condition of painted crayfish is difficult to determine *in situ* and spearfishing may inadvertently cause death or injury of some spawning females.

CHAPTER 3: Evaluation of methods for tracking painted crayfish in the wild

Abstract

Mark-recapture techniques are important tools for estimating population parameters of vagile organisms. However, marking of crustaceans is problematic due to moulting of the exoskeleton. Accordingly, the aim of this chapter was to evaluate three novel (or unconventional) methods of marking or identifying painted crayfish in the wild: ablation, elastomer implants and photographic identification (photo-id). Eighty-five crayfish were captured from Northwest Island and 'marked' using one, two or three of the abovementioned methods. Fifty animals were subsequently recaptured after 6−36 months, giving an overall recapture rate of 59%. Ablation marks (*i.e.* 1−2 small holes cut into one or both uropods) were found to be ineffective for marking painted crayfish, since 90% of the marks became infected or were lost (repaired) within six months. In contrast, 96.5% of elastomer implants were recognisable after 6−36 months, despite numerous episodes of moulting among many of the host animals. With respect to photo-id, exoskeletal colour patterns in painted crayfish were found to be highly polymorphic, individually unique, resistant to ecdysis, and stable through time. It was concluded that both photo-id and elastomer implants are effective methods for tracking painted crayfish over long-term periods.

3.1 Introduction

Tagging of wild organisms is an important tool used by fisheries scientists to estimate population size, movement patterns, growth rates and the effectiveness of restocking programs (Wydoski and Emery 1983; Bergman *et al*. 1992; Bannister *et al*. 1994). Unlike for other fishery resources, however, tagging of crustaceans presents a particular challenge, since any tag or mark that is attached to the exoskeleton is lost during ecdysis (moulting). The service life of paint marks, plastic zip-ties and other external tags is therefore limited to one inter-moult period (*i.e.* weeks to months for most palinurids) (Aiken 1980; Wahle and Fogarty 2006). Previous attempts to overcome this problem resulted in the development of external tags that are sub-skeletally 'anchored' in the musculature (*i.e.* sphyrion, T-bar and streamer tags). However, even these tags are susceptible to ecdysis: annual tag-loss rates are 8% for west Australian lobster (*Panulirus cygnus*, Melville-Smith and Chubb 1997), 36–40% for American lobster (*Homarus americanus*, Ennis 1986; Rowe and Haedrich 2001) and 100% for blue-swimmer crab (*Portunus pelagicus*, McPherson 2002). Moreover, 'anchor' tags have been associated with internal injury (Scarrat 1970), infection (Courtney *et al*. 2001), entanglement (Ennis 1986) and an increase in the likelihood of predation due to physical hindrance or tag conspicuousness (Bergman *et al*. 1992; Linnane and Mercer 1998). Clearly, there is a need to develop more effective methods for tracking individual crustaceans in the wild.

The painted crayfish (*Panulirus versicolor*) is an important fishery resource in the tropical west Pacific region (Pitcher 1993; Munro 2000), including Australia's Great Barrier Reef

(GBR), where it is one of the most popular of all fished species (see Chapter 2). Despite this interest in *P. versicolor*, a comprehensive management scheme is yet to be developed, since there is virtually no information on the biology or ecology of this species. Before this issue can be addressed, however, it is first necessary to develop a reliable method for tracking these animals through space and time. A mark-recapture program can then be used to estimate important population parameters such as growth, mortality and movement patterns. The goal of this chapter, therefore, was to evaluate three new (or unconventional) methods for tracking *P. versicolor* in the wild: ablation, elastomer implants and photographic identification (photo-id).

3.1.1 Ablation

Ablation is the removal or destruction of body tissue in such a manner that individuals can be recognised at a later time. Common examples include ear-notching of domestic cattle, shell-notching of turtles, and fin-clipping of fish (Stonehouse 1978). Although there is some prejudice against these techniques, when performed correctly, they may actually occasion less distress to the animal than the attachment of artificial tags (Stonehouse 1978).

As with any marking method, it is important to minimise discomfort to the animal. Also, ablation marks should not interfere with feeding or movement. In most circumstances, these prerequisites can be achieved by ablating the smallest possible amount of tissue from a region of the body that is relatively insensitive (*i.e.* has a limited supply of nerves) and is not crucial for survival (Stonehouse 1978). To identify individual penaeid shrimps, Balazs (1973) placed small notches in each animal's uropod (a part of the tail-fan). He found that experimental animals retained these marks for at least 45 d, during which time each animal moulted twice. Furthermore, no adverse effects were observed among any of the marked animals (Balazs 1973). In view of this result, ablation may also be useful for marking palinurids such as *P. versicolor*.

3.1.2 Elastomer implants

Elastomer implants are completely internal and thus avoid the problem of tag-loss during moulting. The tag itself consists of a biocompatible, liquid-polymer that cures into a solid within hours of hypodermic injection. When placed in the abdominal musculature of a shrimp or lobster, elastomer implants are clearly visible through the transparent ventral sclerites (Godin *et al*. 1996; Woods and James 2003). Elastomer implants are also flexible, thus reducing physical hindrance, and they do not require specialised detection equipment (like many other internal tags), which enables identification underwater.

Preliminary studies with shrimp (*Penaeus vannamei*), European lobster (*Homarus gammarus*) and spiny lobster (*Jasus edwardsii*) have shown that short-term retention rates of elastomer implants are typically 100%, even after multiple moults (Godin *et al*. 1996; Uglem *et al*. 1996; Woods and James 2003). However, all of these studies were conducted under laboratory conditions. To be sure than elastomer implants are suitable for tracking painted crayfish in the wild, it is therefore necessary to evaluate their performance in the field.

3.1.3 Photographic identification

It is often possible to identify individual animals from variations in natural marks and (or) polymorphic colour patterns. If so, identification may be achieved by comparing photographs (of individual animals) that were taken at different points in time. Although photo-id has been used widely to study vertebrates (*e.g*. fish, Persat 1982; sharks, Anderson and Goldman 1996; whales, Hammond *et al*. 1990), this technique has seldom been used to track the movements of invertebrates, despite the presence of polymorphic colour patterns in many species (*e.g.* Vianna 1986; Whiteley *et al*. 1997).

Given the complexity of colour patterns on the exoskeleton of painted crayfish (Figure 1.1), it may be possible to identify individual animals by photo-id, thereby avoiding altogether the use of artificial tags or marks. However, even if individuals can be distinguished from one another at one point in time, colour patterns may not be consistent over long-term periods, since the exoskeleton is replaced each time the animal moults. Proper evaluation of photo-id must therefore include an assessment of the stability of colour patterns across the moult cycle.

3.2 Materials and methods

3.2.1 Capture and recapture of experimental animals

The study was conducted on the coral reef at Northwest Island (Figure 1.2). The reef at this location is typical of other reefs in the region, having a high diversity and coverage of scleractinian corals with interspersed sand patches. At various depths across the reef, modest numbers of *P. versicolor* can be found wherever suitable dens exist. Anecdotal observations by local fishermen indicate that individuals of *P. versicolor* show considerable site fidelity. The study site (*i.e.* search zone) was therefore confined to an area of *ca*. 60 ha.

Crayfish were captured by hand (with the aid of SCUBA) and restrained in a shallow, water-filled box onboard a nearby support vessel. One, two or three of the tracking methods (*i.e.* ablation, elastomer implants, and photo-id) were applied to each crayfish, depending on logistical constraints (*e.g*. poor lighting sometimes prevented photography). Carapace length (CL) was determined using vernier calipers (± 0.5 mm) and the frequency of moulting inferred from modal growth increments accrued during the inter-census period (Wahle and Fogarty 2006). This whole process took approximately 5 min, after which each crayfish was manually returned to its den.

The study site was censused over ten consecutive days on six occasions: December 2003, June 2004, December 2004, June 2005, December 2005 and December 2006. 'Initial captures' were obtained during censuses 1−5, while 'recaptures' were obtained during censuses 2−6. All recaptured crayfish were processed (*i.e.* examined, photographed and measured) and released again, thus making it possible for multiple recaptures of the same individual at intervals of six months or more. In each case, time-at-liberty (*i.e.* time spent in the wild) was dependent upon the date of initial capture.

3.2.2 Ablation

Using a 5 mm paper punch, one or two holes were applied to the inner ramus of one or both uropods. Given the small size of each hole relative to the size of the entire tail fan, ablation was considered unlikely to effect the behaviour of marked animals (Balazs 1973). Ablation marks were photographed (Sony DSC-P9 digital camera, Tokyo, Japan) before release and after recapture to evaluate the effectiveness of the method. In each case, individual identity was confirmed by secondary marks (*i.e.* elastomer implants or photo-id).

3.2.3 Elastomer implants

Elastomer (Northwest Marine Technology, Shaw Island, U.S.A.) was prepared as specified by the maker and loaded into a U-100 insulin injector (0.33 x 13 mm; Terumo Medical Corporation, Elkton, U.S.A.). A tag was applied by extruding a length of elastomer (15−20 mm) into the abdominal musculature. Care was taken to halt the flow of elastomer before withdrawal of the needle to ensure the tag was completely encased by muscle tissue. Each tag was positioned parallel to (but to one side of) the midline to reduce tag fragmentation and to avoid interference with the abdominal ganglia (Woods and James 2003). All crayfish were tagged twice, with individuality obtained using combinations of different colours (black, fluorescent pink and fluorescent green) and different tag locations (*i.e.* left or right sides in any of the five posterior-most abdominal somites). Annualised tag-retention rates (r) for each period at liberty (6, 12, 18, 24, 30 or 36 months) were then calculated using the equation

$$r = \left[1 - \frac{n_1}{(n_1 + 2n_2)}\right]^{t^{-1}}$$

where n_1 is the number of recaptured individuals retaining one tag, n_2 is the number of recaptured individuals retaining both tags, and t is the time at liberty in years (Seber 1973). Overall tag-retention rate for the three-year study was calculated as the arithmetic mean of the annualised retention rates (Krebs 1999).

To assess changes in the condition of elastomer implants over time, the ventral abdominal region was photographed (before and after recapture) and tag condition was ranked as either 'poor' (rank 1; tag faintly visible due to fragmentation, migration, over-growth or fading), 'good' (rank 2; tag visible but incomplete or showing signs of minor alteration), or 'excellent' (rank 3; tag obvious and in excellent condition). Samples with the same time-at-liberty (*i.e.* 6, 12, 18, 24, 30 or 36 months) were pooled across censuses and the Wilcoxon paired-samples test (Zar 1999) employed to identify differences in tag condition before release and after recapture. Next, a Kruskal-Wallis test (Zar 1999) was used to test for differences in tag condition between groups (*i.e.* to test for effects of time-at-liberty). Homogeneity of initial tag condition was checked *a priori* using the same statistical test.

Crayfish at liberty for 12 months were pooled across censuses and grouped according to moult frequency (0, 1, ≥ 2), gender (male or female), and tag location [anterior abdomen (somites 2−3) or posterior abdomen (somites 4−6)]. The effects of ecdysis, tag location, and gender on tag condition were then assessed using a Mann-Whitney 'U' or Kruskal-Wallis test (Zar 1999). As before, initial tag condition was checked *a priori* for homogeneity.

3.2.4 Photographic identification

A waterproof digital camera (see above) was used to photograph the ventral side of each crayfish. Digital images were downloaded to a computer and viewed using Photostudio software (ArcSoft, Fremont, U.S.A.). Due to the complexity of colour patterns in *P. versicolor*, only the heavily calcified region of the first abdominal sclerite was used for comparative analyses (Figure 3.1). This small section of exoskeleton was chosen because it was (1) easy to define in photographs, (2) always void of spermatophores (tar-spots), eggs and epiphytes, and (3) rarely affected by injury. Secondary marks (ablation marks or elastomer implants) were used to confirm the identity of individual animals.

One photograph was selected to represent each capture and recapture event per crayfish. Next, each photograph was trimmed to remove secondary information, and the remaining portion printed (without enlargement) on high resolution paper. These (trimmed) photographs were assigned a label (depicting the census during which each photograph was taken) and presented to three independent judges who were asked to identify individual crayfish (*i.e.* crayfish that were captured during two or more censuses) based on colour patterns. Errors in identification were recorded as ‘false’ if an incorrect match was made, or ‘missed’ if a correct match went unnoticed.

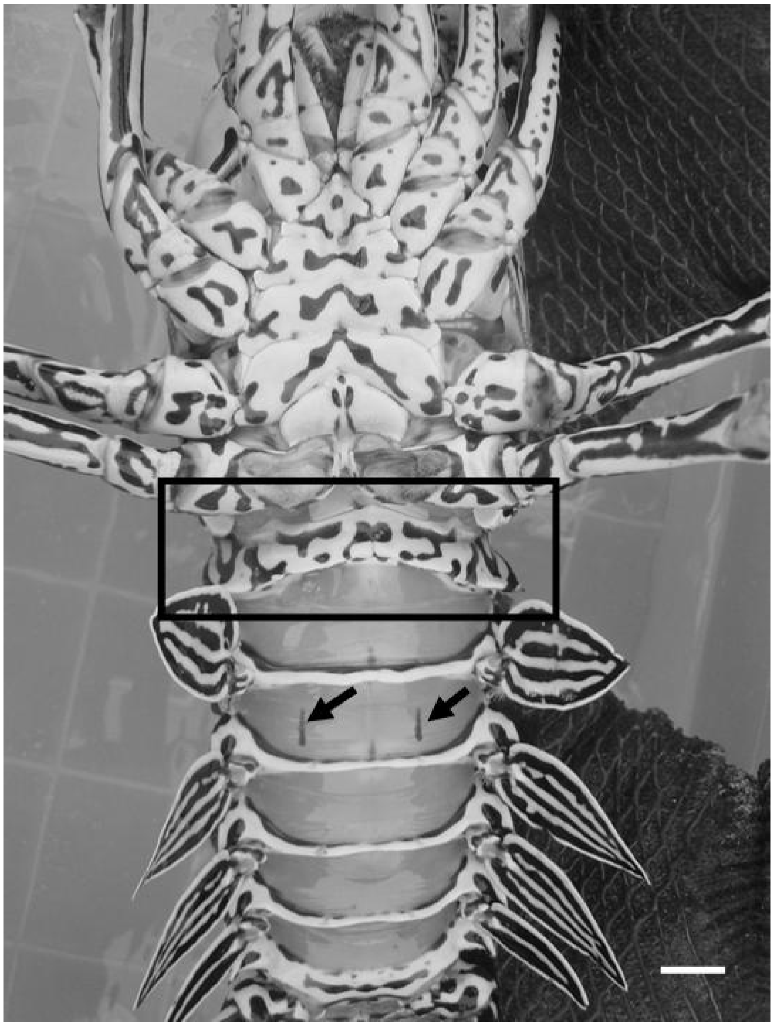

Figure 3.1 Photograph showing the location of the heavily calcified region of the first abdominal sclerite in *Panulirus versicolor*. The inserted *rectangle* defines the portion of each photograph that was excised for reliability analysis. *Arrows* show the location of secondary marks (*i.e.* elastomer implants) that were used to confirm individual identity. Scale bar = 20 mm

3.3 Results

3.3.1 Ablation

Seventeen painted crayfish were marked and released during December 2003. This included 12 males (43−148 mm CL) and 5 females (98−146 mm CL). Ten individuals were recaptured after six months. Of these, only one animal had an ablation mark that was easily discernable. Ablation marks on the remaining animals were either repaired (*n* = 6) or infected (*n* = 3), and were thus difficult to identify (Figure 3.2).

Due to the low retention rate of ablation marks, this method was considered to be ineffective for tracking painted crayfish in the wild. Furthermore, it was considered to be detrimental to the health of some individuals (due to infection). The use of ablation was therefore discontinued after the first census (December 2003).

3.3.2 Elastomer implants

Eighty-five painted crayfish were double-tagged between December 2003 and December 2005. Of these, 37 were male (93–148 mm CL) and 48 were female (94–156 mm CL). Fifty individuals were recaptured after 6−36 months, giving an overall recapture rate of 59%. Only three instances of tag loss were observed, so the estimated annual rate of tag retention (averaged over 3 yr) was 96.5% (Table 3.1).

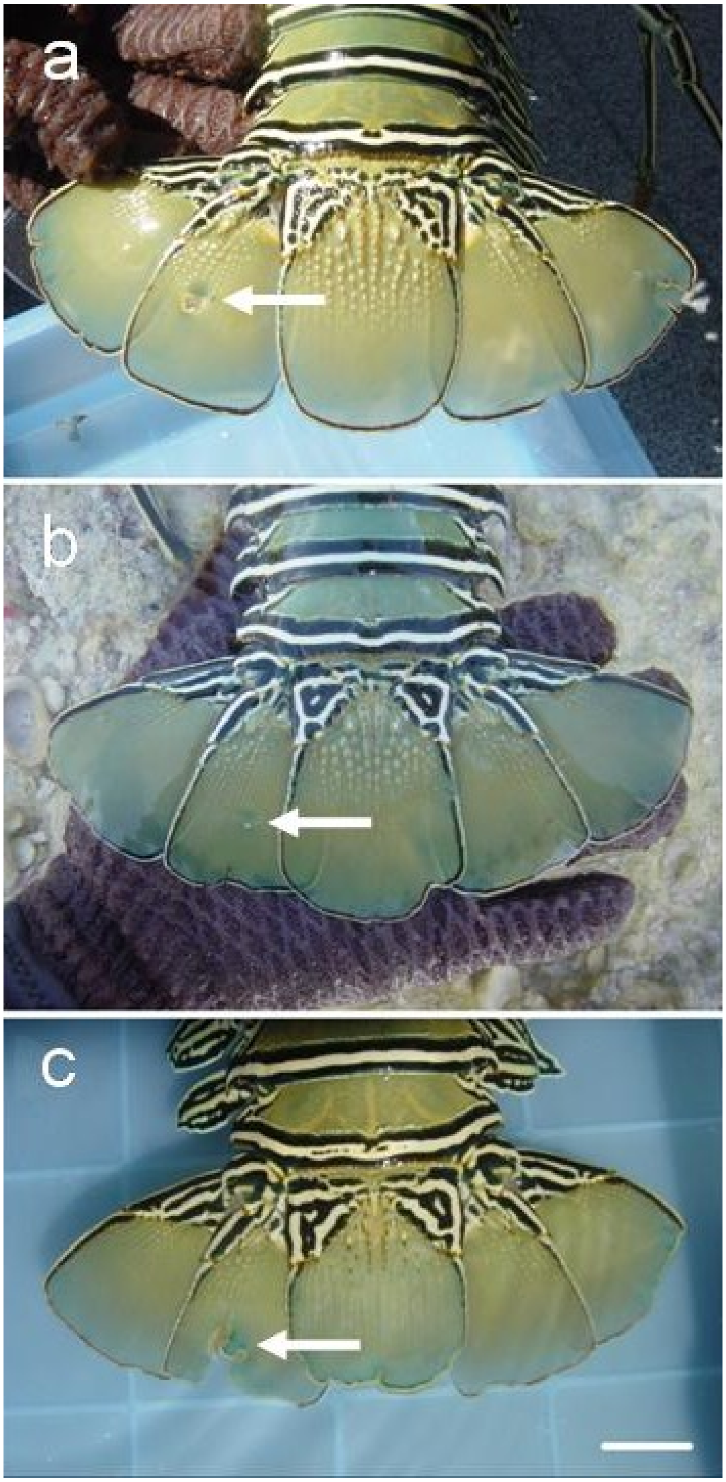

Figure 3.2 Photographs showing (a) retained, (b) repaired and (c) infected ablation marks (indicated by *arrows*) on the left uropods of three *Panulirus versicolor* that were recaptured after six months at liberty. Scale bar = 25 mm

The majority (92%) of tags were easily visible (rank 2 or 3), even after periods of 1−3 yr (Figure 3.3). However, a small but significant decline in median tag condition was detected after periods of 6−36 months (Table 3.2). This decline was primarily caused by fading and (or) fortification of the abdominal tissues surrounding the tag. A few tags fragmented, although in most cases the constituent pieces remained in the same area as the original tag and thus did not interfere with tag interpretation. On two occasions, very small pieces of elastomer migrated into nearby abdominal somites.

Table 3.1

Retention rate of elastomer implants in *Panulirus versicolor* that were recaptured after 6−36 months

Time at liberty (mo)	Size of tagged population[a]	Number of recaptures[a]	Instances of tag-loss	Annualised retention rate (%)
6	85	30	0	100
12	55	7	1	92.3
18	48	8	2	90.2
24	40	3	0	100
30	37	2	0	100
36	35	0	0	100
Total	85	50	3	96.5

[a] Assumes sampling without replacement

Table 3.2

The effect of time-at-liberty on the condition of elastomer implants in *Panulirus versicolor*

Time at liberty (mo)	Number of samples[a]	Tag condition before release	Tag condition after recapture	Significance[b] (*p*)
6	30	3	2	<0.001
12	16	3	2	0.009
18	20	3	2	0.007
24	8	3	2	0.03
≥30	12	3	2	0.01

Tag condition is expressed as the median rank (rank 1 = tag faintly visible due to fragmentation, migration, over-growth or fading; rank 2 = tag visible but incomplete or showing signs of minor alteration; rank 3 = tag obvious and in excellent condition)

[a] Assumes sampling with replacement

[b] Wilcoxon paired-sample test (one-tailed)

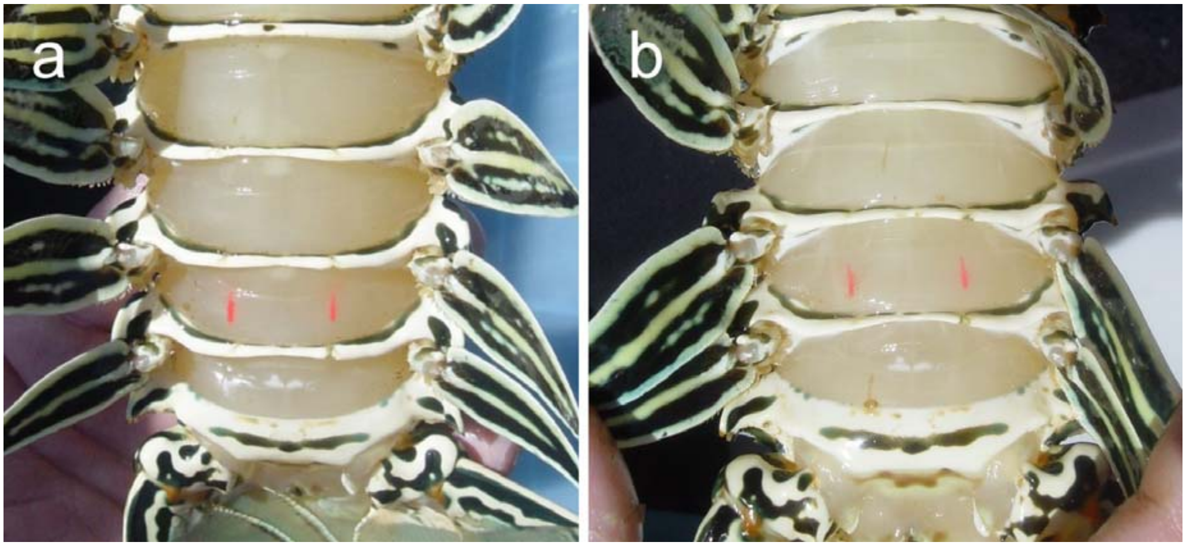

Figure 3.3 Photographs showing the condition of elastomer implants in the fifth abdominal somite of *Panulirus versicolor* before initial release (a) and after 18 months at liberty (b) on the Great Barrier Reef. Tag condition in this individual was rated as ‘excellent’ (rank 3) before release and ‘good’ (rank 2) after recapture (see Materials and methods section for further information on tag condition).

Despite differences in tag condition before release and after recapture (*i.e.* within groups), there was no significant difference in tag condition (after recapture) between groups (Kruskal-Wallis test, $\chi^2_2 = 0.27$, $p = 0.92$). Thus, although tag condition declined after initial implantation (*i.e.* during the first six months at liberty), there were no further declines in tag condition after this time.

Eighty-four percent (42/50) of all recaptured crayfish increased in size (CL) during the inter-census period. Modal growth increments were observed at 2−3, 5−6, and 8−9 mm. These increments were inferred to represent one, two and three moults respectively. After

12 months at liberty, the condition of tags in non-moulted crayfish was not significantly different to the condition of tags in crayfish that moulted one or more times (Table 3.3) (Kruskal-Wallis test, $\chi^2_2 = 0.24$, $p = 0.89$). Thus, moult frequency did not significantly influence tag condition.

Tag condition was not influenced by gender or tag location. After 12 months, tag condition in male crayfish was not significantly different to that in female crayfish (Table 3.3) (Mann-Whitney U test, $U_{10,11} = 50$, $p = 0.69$). Similarly, the condition of tags placed in anterior abdominal somites was not significantly different to the condition of tags placed in posterior abdominal somites (Table 3.3) (Mann-Whitney U test, $U_{10,8} = 38.5$, $p = 0.88$).

Table 3.3

The effect of moult frequency, gender and tag location on the condition of elastomer implants in *Panulirus versicolor* that were recaptured after 12 months

	Moult frequency[a]			Gender		Tag location	
	0	1	≥2	Male	Female	Anterior[b]	Posterior[c]
Tag condition before release	3	3	3	3	3	3	3
Tag condition after recapture	2	2	2	2	2	2	2
Number of samples	7	6	8	10	11	10	8

Tag condition is expressed as the median rank (rank 1 = tag faintly visible due to fragmentation, migration, over-growth or fading; rank 2 = tag visible but incomplete or showing signs of minor alteration; rank 3 = tag obvious and in excellent condition).

[a] Inferred from modal growth increments
[b] Abdominal somites 2–3
[c] Abdominal somites 4–6

3.3.3 Photographic identification

Fifty-six *P. versicolor* were tagged and photographed between December 2003 and December 2005 (Table 3.4). Of these, 28 were male (43–148 mm CL) and 28 were female (94–156 mm CL). Thirty individuals were recaptured after 6, 12, 18, 24, 30 and (or) 36 months, giving an overall recapture rate of 54%. A further three (previously uncaptured) crayfish were photographed during the final census in December 2006.

Ninety percent (27/30) of recaptured crayfish moulted during the inter-census period (inferred from changes in CL). Absolute growth for all crayfish was in the range of 2−22 mm CL, except one small crayfish (initial CL = 43 mm) grew by 37 mm CL.

Colour patterns on the first abdominal sclerite were found to be highly polymorphic, with noticeable intraspecific differences in the size, number, shape and arrangement of pigmented areas (Figure 3.4). All 59 crayfish that were examined could be distinguished on the basis of these characteristics. Colour patterns were also stable over time, irrespective of whether ecdysis had occurred (Figure 3.4). All noticeable changes in colour pattern were very subtle and did not interfere with individual identification.

Two judges rapidly identified 29 of the 30 recaptured crayfish (some of which were recaptured more than once), while the remaining judge identified all of the recaptured crayfish. When the first two judges were shown their ‘missed’ identifications, both agreed that the relevant photographs were obviously of the same individual. There were no ‘false’ identifications by any of the judges.

Table 3.4

Photographic identification of *Panulirus versicolor*: capture and recapture statistics

Capture date	Total number captured[a]	Recapture date	Number recaptured[b]	Time at liberty (mo)
Dec. 2003	7	June 2004	2	6
June 2004	23	Dec. 2004	2	6
Dec. 2004	14	June 2005	4	6
June 2005	17	Dec. 2005	2	6
Dec. 2003	7	Dec. 2004	1	12
June 2004	23	June 2005	3	12
Dec. 2004	14	Dec. 2005	3	12
Dec. 2005	19	Dec. 2006	7	12
Dec. 2003	7	June 2005	4	18
June 2004	23	Dec. 2005	4	18
June 2005	17	Dec. 2006	6	18
Dec. 2003	7	Dec. 2005	2	24
Dec. 2004	14	Dec. 2006	2	24
June 2004	23	Dec. 2006	7	30
Dec. 2003	7	Dec. 2006	1	36
Dec. 2006	21	-	-	-

[a] Includes recaptured individuals

[b] Values sharing the same 'capture date' are not mutually exclusive (some individuals were recaptured more than once)

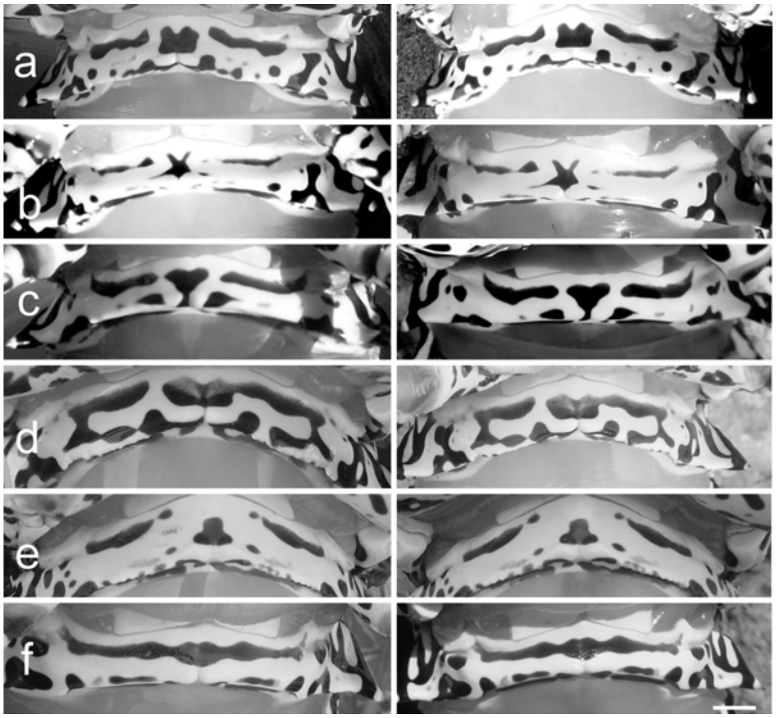

Figure 3.4
Photographs illustrating unique, polymorphic colour patterns in six individuals of *Panulirus versicolor* (a, b, c, d, e and f). The left photograph was taken during initial capture, while the right photograph was taken after recapture. The time at liberty (*i.e.* time between photographs) for these individuals was (a) 6, (b) 12, (c) 18, (d) 24, (e) 30 and (f) 36 months. All six individuals moulted during their time at liberty (inferred from changes in carapace length). Scale bar = 10 mm

3.4 Discussion

3.4.1 Ablation

Despite the utility of ablation for marking other types of organisms (Stonehouse 1978), this study has demonstrated that uropod ablation is of little use for marking painted crayfish in the wild. This is because a high proportion of marks were either lost (repaired) or became infected. The low retention rate probably reflects the extreme regenerative capabilities of these organisms: palinurids can reform damaged or autotomised appendages within one moult cycle (Phillips *et al*. 1980). Thus, the suitability of ablation for marking painted crayfish is probably limited to short-term studies that are conducted under pathogen-depleted conditions (*e.g*. in captivity).

3.4.2 Elastomer implants

The results presented here support previous findings that elastomer implants are effective for tagging crustaceans (Godin *et al*. 1996; Jerry *et al*. 2001; Woods and James 2003). However, the present study makes two important contributions that are additional to those of other studies. Firstly, elastomer implants are shown here to be effective in the wild. This finding is significant because captive conditions can protect tags from factors that would tend to decrease the effectiveness of tags in the wild, such as increased predation and infection (Bergman *et al*. 1992). Secondly, elastomer implants were shown here to be retained for long-term periods (up to 3 yr). Previous to this study, the maximum reported longevity of elastomer implants in crustaceans was only six months (Jerry *et al*. 2001; Woods and James 2003).

The annual retention rate of elastomer implants in wild *P. versicolor* was estimated to be 96.5%. This is much higher than the retention rates reported for T-bar (Melville-Smith and Chubb 1997), streamer (Rowe and Haedrich 2001) and sphyrion tags (Ennis 1986). Although some degradation in the condition of elastomer tags was observed, there were no differences in the condition of tags among crayfish at liberty for 6, 12, 18, 24 or ≥30 months. That is, reductions in tag readability (due to either fading, fragmentation or tissue modification) occur within the first six months, but do not continue after this time. This suggests that elastomer implants would be retained in readable condition for many years, at least in *P. versicolor*.

Tag condition was not affected by moult frequency, gender or tag location. This result supports the notion that elastomer implants are resistant to moulting (Uglem *et al*. 1996; Jerry *et al*. 2001), and confirms the proposition that elastomer tags can be placed in different somites (to increase the number of unique tag combinations) without affecting tag retention or condition (Uglem *et al*. 1996).

Despite qualitative reductions in tag condition after six months, the majority of tags were easily discernible in daylight, either onboard the vessel or underwater. The most visible colour was pink, primarily because it obtained maximum contrast with surrounding tissues. Black, on the other hand, was the least visible colour because it matched the appearance of intramuscular parasites.

The visibility of each elastomer implant was also dependent upon tag size and internal positioning. In particular, the most visible tags were as long as possible and parallel to (but just under) the abdominal sclerites (*i.e.* shallow in depth). Other techniques for improving tag condition include orientating tags parallel to surrounding muscle fibres (Woods and James 2003) and suppressing abdominal movements (*i.e.* tail flicking) immediately after tag implantation (to reduce tag fragmentation). Also, tagging females in the anterior-most abdominal somite avoids the subsequent concealment of tags should the animal become gravid.

Most studies to date have utilised elastomer implants for batch tagging – similarly coloured, single tags have been inserted into equivalent somites of different experimental animals (Jerry *et al*. 2001; Woods and James 2003). One disadvantage of such batch tagging is the loss of information relating to individual animals (*e.g*. growth rate). In this study, combinations of different colours and tag locations were used to distinguish individuals. Up to 405 animals could have been identified with the use of two tags and a choice of three colours. Incidentally, if three tags were used and there was a choice of five colours, the number of possible combinations increases to 15,000. The number of tagged crayfish could also have been doubled by re-using the same combinations in both males and females, since the sex of painted crayfish is readily distinguishable (see Chapter 4). Elastomer implants would thus appear to provide enough individuality to accommodate even a commercial-scale tagging program.

Apart from having excellent retention and good visibility, the ideal tag does not alter behaviour, survival, or the potential for recapture (Bergman *et al*. 1992). The characteristics of elastomer implants are such that they are likely to satisfy all of these criteria. Firstly, elastomer tags are small (in comparison to the overall size of the host) and flexible, thus minimizing physical hindrance. Secondly, they are internally compartmentalised, thus reducing the likelihood of infections that are common to other types of tags. Thirdly, elastomer implants can be discretely positioned on the ventral side of the host − an aspect that would tend to reduce tag conspicuousness among potential predators. It is also unlikely that elastomer implants interfere with the host's metabolism, since elastomer is medically-approved and non-toxic to humans (Northwest Marine Technology, Shaw Island, USA). This is an important consideration for tagging animals that may be consumed.

Despite the abovementioned benefits, one disadvantage of using such small, internal tags is that potential hosts must be captured and handled to search for tags. This may prove unacceptable for some applications (*e.g.* broodstock identification for aquaculture). Another disadvantage is that ready-to-use (*i.e.* pre-mixed) elastomer has a short shelf-life at ambient temperature, especially in the tropics (*ca*. 1 hr). One consequence is that elastomer implants must be continually prepared. However, this disadvantage is at least partially offset by the ease of application and cost effectiveness of elastomer tags.

3.4.3 Photographic identification

Two assumptions of photo-id in capture-recapture studies are that (1) colour patterns are distinctive enough to ensure that all individuals in a population can be identified with a high degree of accuracy, and (2) colour patterns are permanent enough to allow all individuals to be identified through time (Pennycuick 1978). In relation to the first assumption, it is clear that colour patterns in painted crayfish are highly polymorphic and unique to individuals, at least for the 59 animals examined. Furthermore, these animals were distinguished relatively easily (even though only a small section of exoskeleton was considered), thus suggesting that photo-id could be used to identify many, perhaps thousands of different animals. One explanation for the degree of polymorphism in painted crayfish is that external colour patterns function in intraspecific recognition, as has been suggested for other crustacean species (Dunham 1978; Vannini and Gherardi 1981; Hall-Spencer *et al*. 1999).

With respect to the second assumption, it is evident that colour patterns in painted crayfish are stable over time and resistant through ecdysis. Given that growth increments in adults of this species are commonly 2−3 mm CL (see Chapter 4), it appears that most recaptured crayfish moulted 2−7 times during the inter-census period. The case of the small individual (CL = 43 mm at capture and 80 mm at recapture) indicates that terminal colour patterns are attained well before the establishment of reproductive maturity (78−88 mm CL; see Chapter 4). These results are consistent with the notion that colour patterns are both genetically determined (Ghidalia 1985) and permanent (at least in sub-adult and adult crayfish).

The use of photo-id in capture-recapture studies can incur two types of errors: false matches and missed matches (Pennycuick 1978). Considering the degree of polymorphism in painted crayfish, errors of the former type were unlikely to have been encountered. In contrast, errors of the latter type were probable, since the judges were inexperienced, and each was required to perform over 4,000 manual comparisons. Furthermore, some matches were less obvious than others, not because of indistinct colour patterns, but because the photographs varied in quality (*e.g.* angle and focus). The probability of missed matches could therefore be substantially reduced by (1) training of personnel in techniques of identification, (2) using computer programs to match photographs (*e.g.* Arzoumanian *et al.* 2005), and (3) acquiring higher quality photographs. This would ensure that all crayfish in the population have an equal chance of being correctly identified as a 'recaptured' animal.

The primary advantage of using photo-id in capture-recapture studies is that it circumvents the need for tags, thereby avoiding the logistical, ecological and ethical problems of attaching an artificial object to a wild animal. However, using photo-id also has disadvantages. Firstly, it removes the potential for tag reporting by the public, since there is no tag to return. Secondly, it is labour intensive, especially when large numbers (*i.e.* thousands) of animals are involved.

3.4.4 Conclusion

It is concluded that elastomer implants and photo-id are highly effective methods for tracking painted crayfish in the wild. In particular, both methods overcome the problem of tag-loss during moulting and accommodate the need for individual identification. Furthermore, both methods are unlikely to influence growth, behaviour or survival of individuals. It is predicted, therefore, that elastomer implants and photo-id will be useful for estimating the population parameters of this species *via* a mark-recapture program.

CHAPTER 4: Growth and reproduction

Abstract

The growth and reproductive characteristics of painted crayfish at Northwest Island (Great Barrier Reef; GBR) were investigated *via* a three-year, mark-recapture program. Ovigerous female crayfish were captured in both summer and winter, suggesting this species has a protracted spawning period. Although some females reproduced *in situ*, the majority of mature females appeared to emigrate during summer, resulting in a male-biased local population. Overall sex-ratios, however, did not differ from unity during the study period. Moult interval for larger (>125 mm carapace length; CL) and smaller (90−125 mm CL) individuals was estimated to be 326 ± 31 and 159 ± 18 d, respectively. Growth increment was estimated to be 2−3 mm CL and appeared to be constant across the range of sizes examined (98−153 mm CL). Growth rate was asymptotic, with the lifetime growth trajectory of *P. versicolor* well defined by a von Bertalanffy growth model (L_∞ = 144.7 mm CL; K = 0.27 yr^{-1}; t_0 = -0.18 yr). A separate group of painted crayfish (collected from the Townsville region of the GBR) revealed that males and females attained reproductive maturity at 88 and 78 mm CL, respectively. These growth and reproductive parameters will be useful for optimizing population models and management strategies for this valuable fishery resource.

4.1 Introduction

Most well-managed fisheries utilise a combination of size limits, catch limits, marine reserves and (or) closed seasons to regulate catch and effort (Chubb 2000; Melville-Smith *et al*. 2000). For maximum effectiveness, these regulations should be designed according to the growth and reproductive characteristics of the resource. For example, catch limits should be set at or below the maximum sustainable yield, which, in turn, is dependent upon the growth rate of the stock (*e.g*. yield per recruit models) (King 1995). Similarly, size limits should be set at or above the size at first maturity (SFM), thereby ensuring that all individuals in the population have the opportunity to breed before harvest (King 1995). Defining the growth and reproductive characteristics of an exploited species is therefore an important step toward successful management of a spiny lobster fishery.

The reproductive status of spiny lobsters is often defined in terms of the presence or absence of spermatophores (*i.e.* sperm ‘packets’ that are attached to the sternites of female individuals during mating) and (or) the presence or absence of oviposited eggs (*i.e.* eggs that are attached to the filamentous setae of female individuals) (Aiken and Waddy 1980; Chubb 2000). This is because both spermatophores and oviposited eggs are macroscopic, lasting in nature, and can be observed without sacrificing the animal (*i.e*. after hand capture).

Unlike other fishery resources, crustaceans exhibit discontinuous growth. As a result, growth trajectories are step-like, resulting from a combination of growth increments at each moult, and the time interval between moults (Aiken 1980; Pitcher 1993). Among palinurids, it is typical for moult intervals to increase and growth increments (expressed as a proportion of body size) to decrease with each successive moult, such that the rate of growth slows with increasing size (Aiken 1980; Pitcher 1993). For most species, growth increments are small in comparison to maximum size, while moult intervals are short in comparison to maximum age (Mauchline 1977). This enables growth trajectories to be adequately described by von Bertalanffy (1938) growth models (Morgan 1980; Wahle and Fogarty 2006).

The painted crayfish (*Panulirus versicolor*) is an important catch component of the recreational spearfishery on the Great Barrier Reef (GBR) (see Chapter 2). However, current management strategies for this species are based entirely on precautionary principles rather than quantitatively-derived population parameters, since these are yet to be determined. The aim of this chapter was therefore to (1) describe the SFM and reproductive periodicity of *P. versicolor*, (2) describe the growth characteristics of this species in terms of increment and interval, and (3) estimate the growth trajectory of *P. versicolor* using the von Bertalanffy (1938) growth function.

4.2 Materials and methods

4.2.1 Mark-recapture program

Animals used in this study were the same as those described in Chapter 3, excluding the animals bearing injury or infection. As such, the reader should consult section 3.2.1 for details regarding the study site, capture method, and tagging technique.

When a crayfish was captured, its gender was determined by the presence of externally dimorphic features (*e.g.* males and females have gonopores at the bases of the fifth and third walking legs, respectively; Phillips *et al.* 1980). For female crayfish, reproductive status was recorded as (1) ovigerous (bearing oviposited eggs), (2) mated (bearing a spermatophore on the sternite) or (3) non-mated (bearing neither eggs nor spermatophore). Carapace length (CL; between the sub-orbital ridge and the posterior, dorsal edge of the carapace) was measured using vernier calipers (± 0.5 mm).

The study site (60 ha of coral reef at Northwest Island) was censused for ten consecutive days on six occasions: December 2003, June 2004, December 2004, June 2005, December 2005 and December 2006 (December and June fall within the Austral summer and winter, respectively). To ensure that sampling effort was consistent among censuses, all dens in the study area were searched everyday. All recaptured crayfish were measured for size and released again, thus making it possible for multiple recaptures of the same individual at approximately six month intervals. To avoid bias from repeatedly recapturing some of the same individuals during successive censuses, only the data from newly-encountered individuals were used in the analysis.

4.2.2 Data analyses

To investigate size-specific differences in growth and reproductive parameters, crayfish were assigned to one of two size classes and analysed separately ('larger', >125 mm CL; 'smaller', 90−125 mm CL). The number and breadth of these size classes were chosen *a posteriori* to ensure both adequate replication and a balanced sampling design (Zar 1999). It was not possible to adequately sample crayfish <90 mm CL because crayfish of this size rarely inhabit offshore reefs such as Northwest Island (see Chapter 5).

Absolute growth (mm) was calculated as the change in CL during the inter-census period, while growth rate (mm yr^{-1}) was calculated as the change in CL over the entire period at liberty (6−36 months). When estimating size-specific growth rates, individuals that advanced into the larger size class during the inter-census period were excluded from the analyses unless an estimate of growth rate could be obtained either wholly before or after size-class transition.

Polymodal growth distributions of similarly sized crayfish were used to identify animals that moulted one to three times, with the first mode reflecting a single growth increment and subsequent modes reflecting two or more growth increments. Moult interval was calculated as the average time at liberty of individuals that moulted once only during an inter-census period (Robertson and Butler 2003).

Growth rate was assumed to follow the von Bertalanffy (1938) growth function:

$L_t = L_\infty[1 - e^{-K(t-t_0)}]$

where L_t is carapace length at age t, L_∞ is the mean asymptotic carapace length, K (growth coefficient) is the rate at which L_∞ is approached, and t_0 is the hypothetical age at zero length (estimated by constraining the y-axis intercept). The y-axis intercept was assigned a value of 7 mm, based on the size of new recruits of *P. versicolor* at Minicoy Atoll, Indian Ocean (Pillai *et al*. 1985). This value is similar to (and thus supported by) the size at settlement of many other palinurid lobsters throughout the Indo-Pacific region (Phillips and Sastry 1980; Pitcher 1993).

Given the time at liberty was short, the values of L_∞ and K were calculated as per Gulland and Holt (1959) using the equation:

$(\Delta L_c/\Delta t) = a + bL_m$

where ΔL_c is the change in carapace length during Δt (the time at liberty), and L_m is the mean carapace length during Δt. The letters a and b represent the (y-axis) intercept and slope of the regression line (respectively), such that K is equivalent to –b, and L_∞ is equivalent to –a/b.

To enable prediction of the von Bertalanffy growth curve over the entire size range of *P. versicolor*, data from six captive juveniles that were reared by Kuthalingam *et al*. (1980) were included in the analysis. It must be noted, however, that these crayfish were studied in captivity, and that they originated from a distant locality (Vizhinjam, India).

Nonetheless, it was thought that any potential bias would be small in comparison to that incurred by extrapolating from the lower limit of sample data to t_0 (King 1995).

4.2.3 Statistical analyses

Frequency distributions were analysed using χ^2 tests. In some cases, size classes were aggregated to ensure that mean expected frequencies were greater than six (Zar 1999). Sex- and size-specific growth rates were compared using Student's *t* test, while mean sizes of female reproductive stages were assessed using one-way ANOVA (Zar 1999). When nonparametric data were encountered, a Mann-Whitney 'U' test was used (Zar 1999). The significance of a regression line was evaluated using the least squares method, and two regression lines were compared using the *t*-test procedure described by Zar (1999).

4.2.4 Size at first maturity

Except for the occasional individual, juvenile crayfish are absent from Northwest Island (Author's personal observation). It was therefore not possible to estimate SFM using samples obtained by the mark-recapture program. As such, a separate sample of 53 crayfish (juveniles and adults) were collected from Middle Reef, Palm Island and Walker Reef, which are 2, 20 and 60 km (respectively) from the mainland coast near the city of Townsville. Crayfish were captured from shallow rocky or coral reefs either by spearfishing or by anaesthetisation (10% clove oil in ethanol).

Size at maturity for males and females was based on initiation of allometric growth of the third and fifth walking legs, respectively ('intersect method'; George and Morgan 1979). Leg length was plotted against CL and separate regression lines were constructed for juvenile and adult crayfish. If the slopes of the two regression lines were significantly different (as determined by a *t* test; Zar 1999), the point of intersection was interpreted as the SFM (George and Morgan 1979; Sharp *et al*. 1997; Robertson and Butler 2003). Individuals that were close to the predicted SFM (*i.e.* 75−90 and 70−85 mm CL for males and females, respectively; George and Morgan 1979; MacDonald 1982) were excluded from the analysis because their state of maturity was not determined.

A standard tape-measure was used to measure leg length to the nearest millimetre. Leg length was defined as the distance between the tip of the dactyl and the proximal margin of the basis, measured along the ventral surface. Care was taken to avoid damaged or regenerating legs.

4.3 Results

4.3.1 Mark-recapture program

Eighty-five *P. versicolor* were tagged and released between December 2003 and December 2005. Of these, 37 were male and 48 were female, with the ratio of males to females not significantly different from 1:1 (χ^2 test, $\chi^2_1 = 1.18$, $p > 0.25$). The size range of captured crayfish was 93−148 mm CL for males and 94−156 mm CL for females, with a homogeneous distribution of males and females across size classes (χ^2 test, $\chi^2_4 = 1.80$, $p > 0.75$) (Figure 4.1). Fifty tagged individuals were recaptured after 6−36 months, giving an overall recapture rate of 59%.

The mean sizes of non-mated, mated and ovigerous female crayfish were not significantly differently (ANOVA, $F_{2,45} = 2.20$, $p = 0.12$) and the distribution of reproductive stages among females was not related to size (χ^2 test, $\chi^2_2 = 1.80$, $p > 0.25$) (Figure 4.2). However, the distribution of reproductive stages was found to vary with season (χ^2 test, $\chi^2_3 = 17.8$, $p < 0.001$) (Figure 4.3). All the females captured in December (summer) were either mated or ovigerous, while the majority of females captured in June (winter) were non-mated. Furthermore, there were approximately four times more females captured in winter than in summer. In contrast, the number of males captured in each season was relatively stable. As a result, the ratio of males to females during winter was *ca*. 1:2, while in summer the ratio changed to *ca*. 2:1.

Growth trajectories for individual crayfish were variable, although a distinct decline in growth rate was apparent once a CL of *ca*. 130 mm was attained (Figure 4.4). In fact, smaller crayfish (90−125 mm CL) grew significantly faster than did larger crayfish (>125 mm CL) (*t* test, $t_{45} = 5.41$, $p < 0.001$). Mean growth rates for the two groups were 8.1 ± 0.7 mm yr^{-1} and 2.2 ± 0.5 mm yr^{-1}, respectively. There was no significant difference in mean growth rates of male and female crayfish, regardless of body size (larger crayfish, $t_{21} = 0.69$, $p = 0.50$; smaller crayfish, $t_{19} = 0.22$, $p = 0.35$).

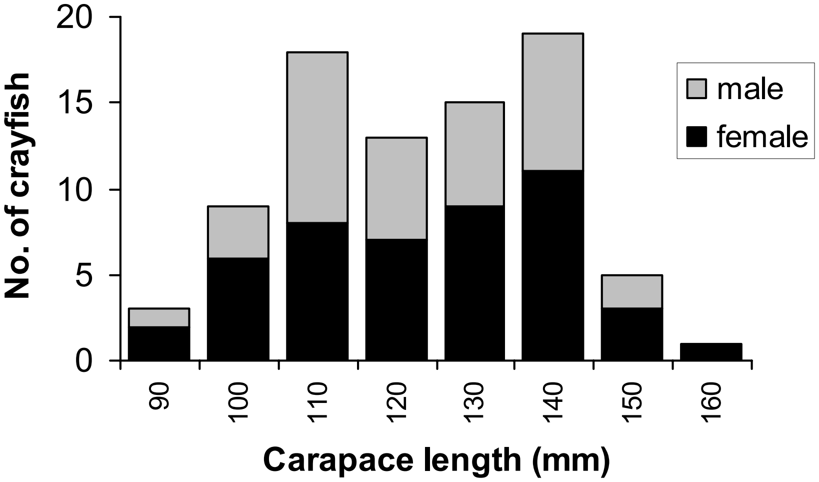

Figure 4.1 Length-frequency distribution of male and female *Panulirus versicolor* that were captured at Northwest Island between December 2003 and December 2005. The *x*-axis labels are size-class midpoints.

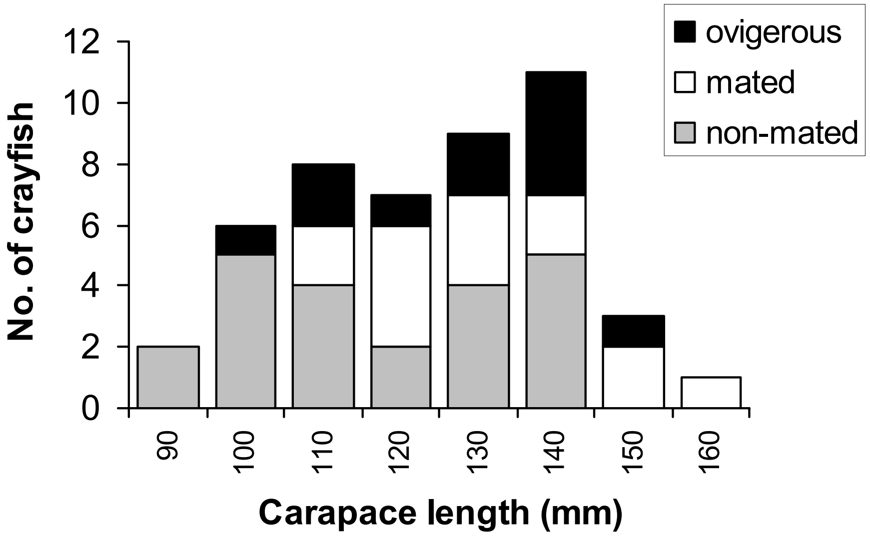

Figure 4.2 Length-frequency distribution of reproductive stages among female *Panulirus versicolor* that were captured at Northwest Island between December 2003 and December 2005. See section 4.2.1 for definitions of reproductive stages. The *x*-axis labels are size-class midpoints.

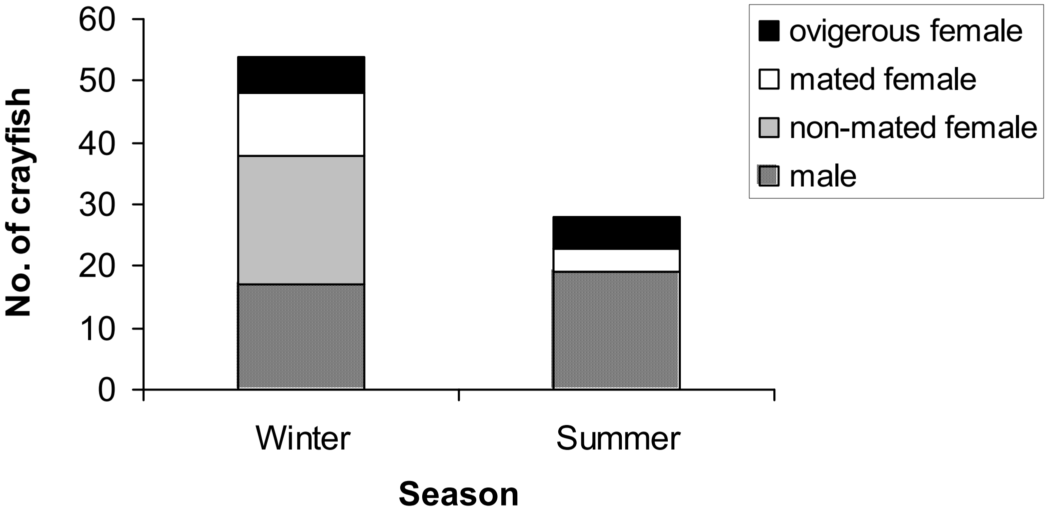

Figure 4.3 Seasonal distribution of reproductive stages in *Panulirus versicolor* at Northwest Island. Winter surveys were conducted in June of 2004 and 2005 while summer surveys were conducted in December of 2003 and 2004. Data collected in December of 2005 and 2006 were excluded to ensure equal sampling effort among seasons.

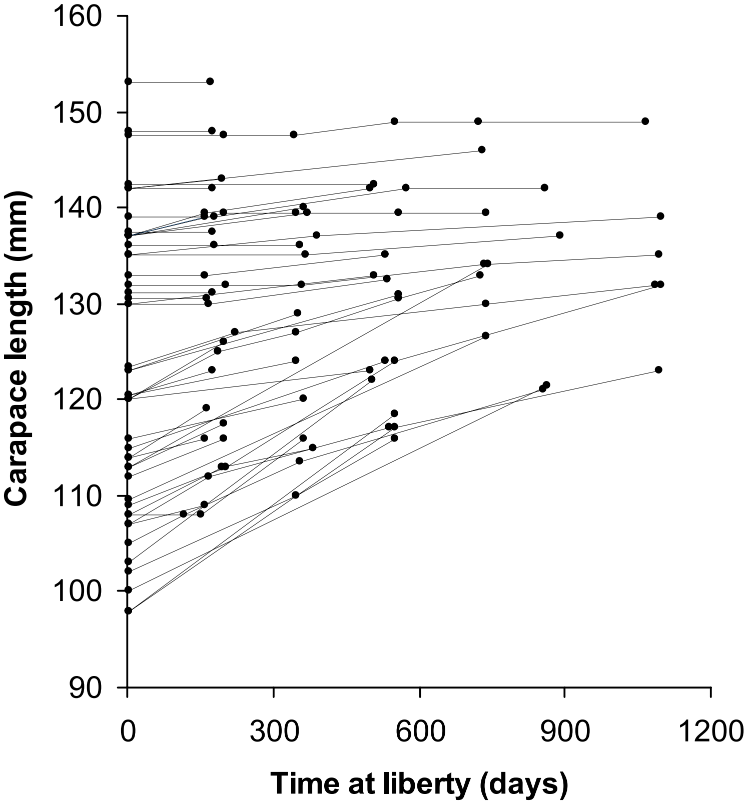

Figure 4.4 Growth trajectories of individual *Panulirus versicolor* that were recaptured at Northwest Island between December 2003 and December 2006. Note the distinct difference in growth rates of smaller (90−125 mm CL) and larger (>125 mm CL) crayfish.

Eight crayfish (all of which were larger) did not grow at all during the period between first release and last recapture. The remaining 42 crayfish increased in size, with absolute growth for most of these individuals in the range of 2−8 mm CL (*n.b.* no crayfish were observed to grow by increments <2 mm CL). For smaller crayfish, three modal frequencies were observed (2−3, 5 and 8 mm CL; Figure 4.5a), suggesting that the growth increment for these animals was approximately 2.7 mm CL (*i.e.* the largest common denominator). A single distinct mode occurred at 2−3 mm CL for larger crayfish (Figure 4.5b), thus suggesting that larger *and* smaller crayfish had a similar growth increment.

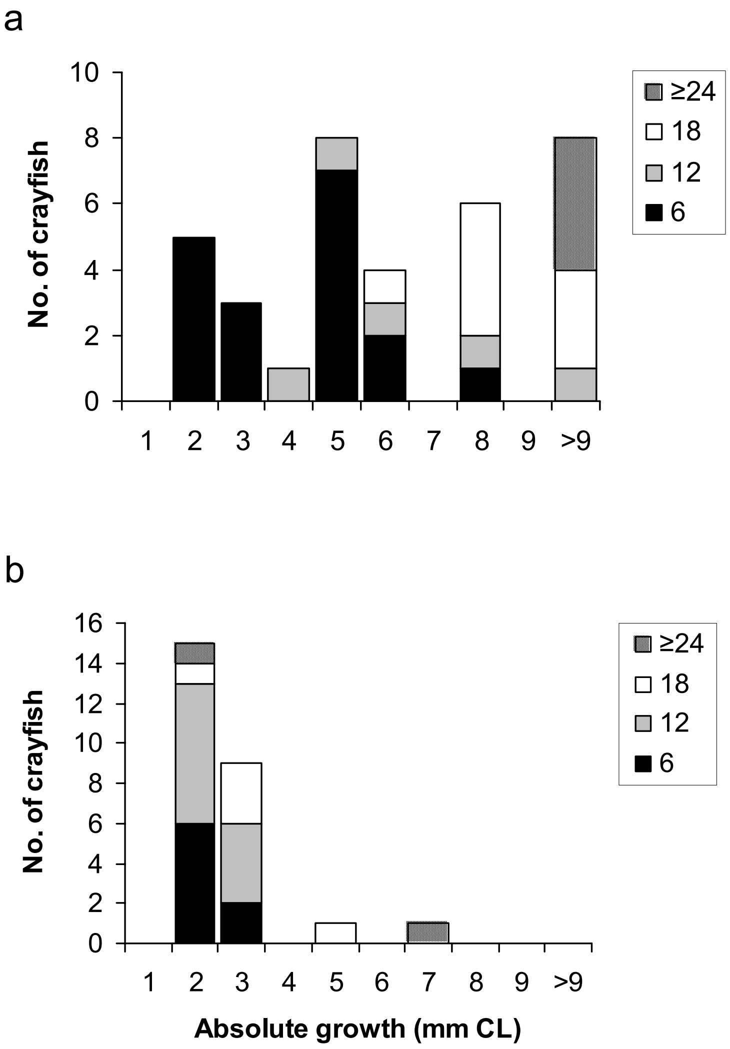

Figure 4.5 Absolute growth of (a) smaller (90−125 mm CL) and (b) larger (>125 mm CL) *Panulirus versicolor* that were recaptured at Northwest Island between December 2003 and December 2006. Individual crayfish were at liberty for 6, 12, 18 or 24−36 months (see legend), depending on the date of release and recapture. Consecutive modal frequencies were assumed to represent one, two and three moult increments, respectively.

Eight smaller crayfish and 24 larger crayfish were estimated to have moulted once only during the inter-census period (*i.e.* their absolute growth was 2−3 mm CL; Figure 4.5). The average time at liberty for these individuals (*i.e.* the moult interval) was 159 ± 18 days and 326 ± 31 days, respectively. For crayfish recaptured after six months, the median sizes of moulted and non-moulted individuals (114 and 137 mm CL, respectively) were significantly different (Mann-Whitney U test, $U_{16,14} = 24.5$, $p < 0.001$; Figure 4.6).

The relationship between body size and growth rate in *P. versicolor* was significant (ANOVA, $F_{1,85} = 651$, $p < 0.001$), as illustrated by a Gulland-Holt plot (Figure 4.7a). The regression equation that describes this relationship was calculated to be:

growth rate (mm yr^{-1}) = 39.2 – 0.27 × CL

with a co-efficient of determination (r^2) of 0.89. When the data from Kuthalingam *et al.* (1980) were excluded from the analysis (Figure 4.7b), the Gulland-Holt regression equation did not change significantly (for slope b, $t_{88} = 0.53$, $p > 0.5$; for intercept a, $t_{89} = 0.48$, $p > 0.5$). The von Bertalanffy growth parameters L_∞, K and t_0 were calculated to be 144.7 ± 1.5 mm, 0.27 ± 0.01 yr^{-1} and -0.18 ± 0.01 yr, respectively (Figure 4.8).

4.3.2 Size at first maturity

The relationship between CL and third leg length was significant for both juvenile male crayfish (ANOVA, $F_{1,8} = 89.7$, $p < 0.001$) and adult male crayfish (ANOVA, $F_{1,14} = 511.8$, $p < 0.001$) (Figure 4.9a). The respective regression equations for the two groups were:

leg length (mm) = 1.51 × CL(mm) − 2.86

leg length (mm) = 4.83 × CL(mm) − 296

The slopes of the two lines were significantly different (t test, $t_{22} = 42.7$, $p < 0.001$), indicating that the pattern of leg growth switched from isometric to (positive) allometric. The point of intersection was calculated to be 88 mm CL, which is the estimated SFM for male crayfish.

The relationship between CL and fifth leg length was significant for both juvenile female crayfish (ANOVA, $F_{1,9} = 253.8$, $p < 0.001$) and adult female crayfish (ANOVA, $F_{1,14} = 68.4$, $p < 0.001$) (Figure 4.9b). The respective regression equations for the two groups were:

$$\text{leg length (mm)} = 1.64 \times \text{CL(mm)} - 5.55$$

$$\text{leg length (mm)} = 0.93 \times \text{CL(mm)} + 50.0$$

The slopes of the two lines were significantly different (t test, $t_{23} = 3.78$, $p < 0.001$), indicating that the pattern of leg growth switched from isometric to (negative) allometric. The point of intersection was calculated to be 78 mm CL, which is the estimated SFM for female crayfish.

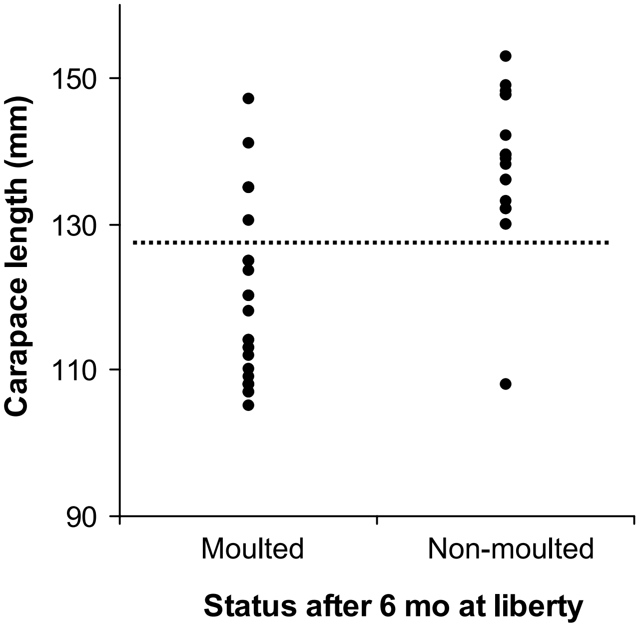

Figure 4.6 Carapace length (CL) and moult status of *Panulirus versicolor* after six months at liberty. Moult status was inferred from changes in CL (or lack thereof). The horizontal line delimits the two artificial size categories noted in Figure 4.4 ('smaller', 90−125 mm CL; 'larger', >125 mm CL).

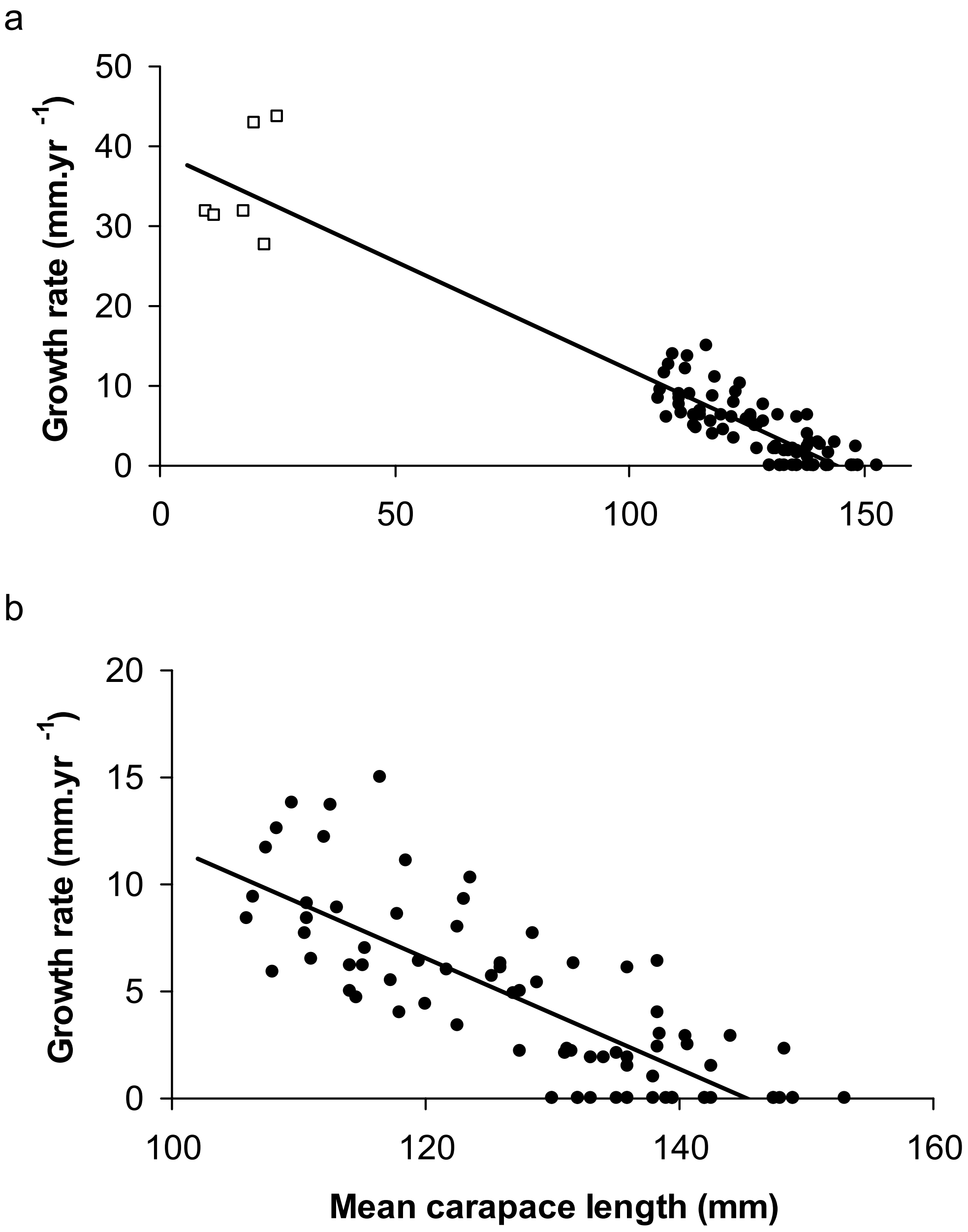

Figure 4.7 (a) Gulland-Holt plot illustrating size-specific growth rates of *Panulirus versicolor* that were sampled during this study (*black circles*) or by Kuthalingam *et al.* (1980) (*hollow squares*). (b) Enlarged panel showing data from this study only. See text for regression parameters and co-efficient of determination.

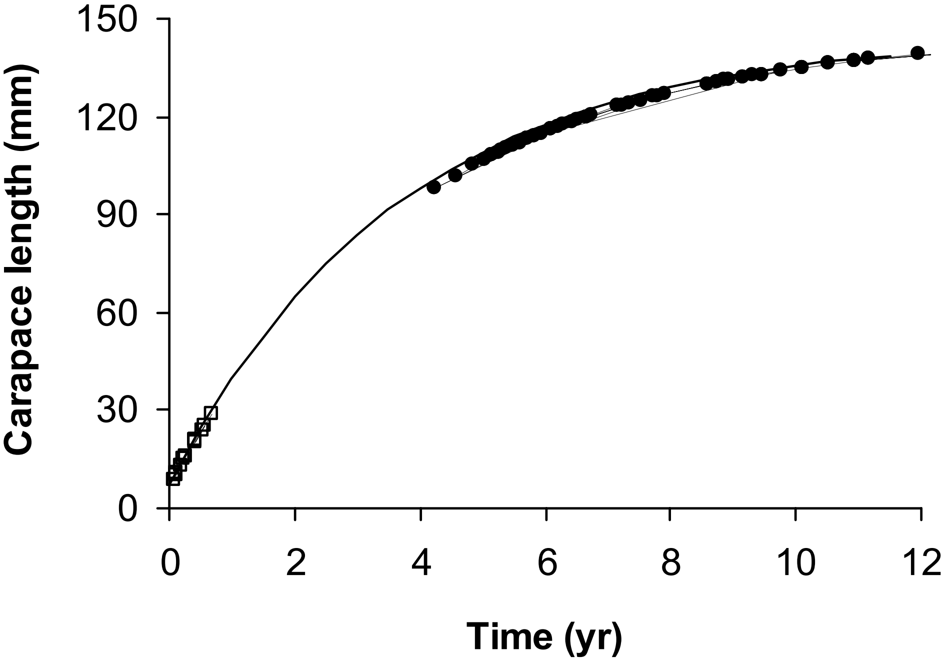

Figure 4.8 Predicted lifetime growth trajectory of *Panulirus versicolor* (*curved line*). The von Bertalanffy growth parameters defining this trajectory are 144.7 mm (L_{∞}), 0.27 yr^{-1} (K) and -0.18 yr (t_0). Individual growth trajectories of six captive juveniles (*hollow squares*) and 43 wild (tagged) adults (*black circles*) are also shown. Juvenile data are from Kuthalingam *et al*. (1980).

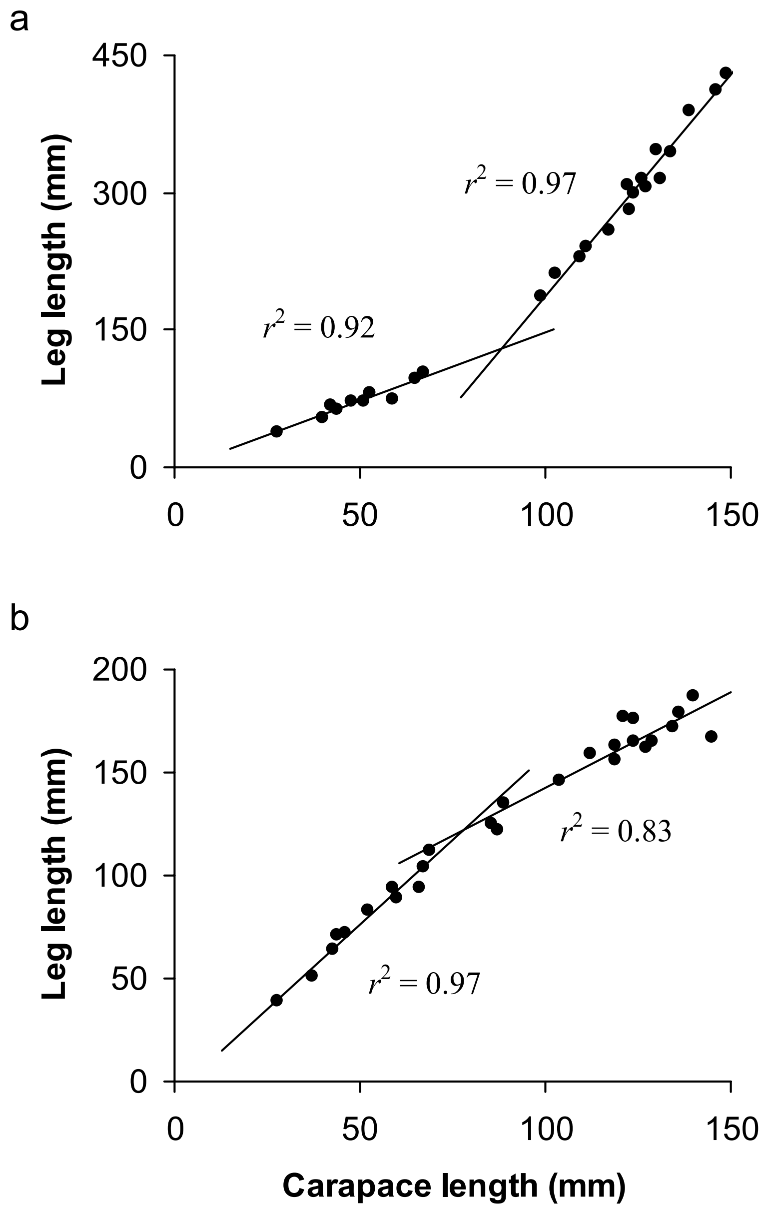

Figure 4.9 Initiation of allometric growth by (a) the third walking leg of males and (b) the fifth walking leg of females of *Panulirus versicolor*. Separate regression lines were constructed for juvenile and adult crayfish, and the point of intersection was interpreted as the size at first maturity (SFM). Displayed next to each regression line is the co-efficient of determination (r^2).

4.4 Discussion

Despite unity in overall sex ratios, the relative abundance of female crayfish at Northwest Island was seasonally variable; female crayfish were numerically dominant in winter, while male crayfish were numerically dominant in summer (Figure 4.3). Seasonal variations in sex ratios have been reported for several other palinurids (*e.g. Panulirus argus*, *Panulirus ornatus*, *Jasus edwardsii*), and often reflect the movement of female crayfish to other reef habitats (Kanciruk 1980; MacDiarmid 1991) or even distant reefs (MacFarlane and Moore 1986). The adaptive value of these movements is postulated to increase female survival during the period of egg incubation, as well as enhance the dispersion (or retention) of larvae (Herrnkind 1980; Kanciruk 1980; MacFarlane and Moore 1986). With regard to *P. versicolor*, it seems that some female crayfish reproduced locally, but the majority migrated to other habitats or reefs. Their destination remains unknown, but given the importance of protecting spawning stocks of *P. versicolor*, this represents an important topic for future research.

The occurrence of ovigerous females in both June and December suggests that reproductive activity in painted crayfish is protracted, or perhaps even continuous. Unlike temperate palinurids, which generally have a well-defined reproductive season, year round spawning is common among tropical species (Chubb 2000; MacDiarmid and Sainte-Marie 2006). Interestingly, MacDonald (1982) found that *P. versicolor* from Palau (7^{o} 30’ N, 134^{o} 30 E) also had a continuous breeding season, although the proportion of ovigerous females in artisanal catches was much higher in autumn (October) than it was in summer (August). In the present study, higher proportions of mated and ovigerous females were captured in December than in June, suggesting that summer is more important (in terms of reproductive activity) than winter for *P. versicolor* at Northwest Island. Regional variations in reproductive seasonality occur in other palinurids and probably relate to differences in environmental factors, particularly water temperature and photoperiod (Pitcher 1993; Chubb 2000; MacDiarmid and Sainte-Marie 2006). Given the immense size of the GBR (approximately 15^{o} of latitude), it is likely that patterns of reproductive activity in *P. versicolor* vary from end to end. If so, seasonal closures designed to protect spawning stocks would need to be either very broad or regionally adapted.

Using the intersect method, the SFM of male and female painted crayfish was estimated to be 88 and 78 mm CL, respectively (Figure 4.9). Two previous studies have also estimated the SFM of this species: MacDonald (1982) found the SFM of female crayfish from Palau was 82 mm CL, while George and Morgan (1979) found the SFM of male and female crayfish from Western Australia was 72 and 65 mm CL, respectively. George and Morgan (1979) used the intersect method (as did the present study), while MacDonald (1982) defined SFM as the size of the smallest ovigerous female in local, artisanal catches. The latter method yields biased results if mature and immature crayfish of the same size vary in their catchability, or if one atypical female matures earlier than other females in the population (Chubb 2000; MacDiarmid and Sainte-Marie 2006). Thus, it is difficult to compare MacDonald's (1982) results with those of the present study.

It is apparent that painted crayfish from Queensland mature later than conspecifics from Western Australia (*cf*. George and Morgan 1979). Regional variations in SFM may reflect differences in environmental conditions such as water temperature, food availability, or conspecific density (Chubb 2000; MacDiarmid and Sainte-Marie 2006). Fishing pressure can also influence SFM by selecting against faster growing individuals (Chubb 2000; MacDiarmid and Sainte-Marie 2006). Unfortunately, the relative intensity of fishing pressure in Queensland *versus* Western Australia is not known.

It is interesting that SFM was slightly greater for males (88 mm CL) than or females (78 mm CL). The same pattern has been found in almost all species of palinurids investigated to date (MacDiarmid and Sainte-Marie 2006). Initially, it was hypothesised that males needed to be larger than females to facilitate mating (Aiken and Waddy 1980), since the male must pull the female onto his body to transfer the spermatophore (Lipcius *et al*. 1983). However, sex-specific differences in SFM may instead be due to intense male-male competition for receptive females (Atema and Cobb 1980; Childress and Jury 2006) or females' preference for larger males that bear larger spermatophores (MacDiarmid and Butler 1999).

If protection of a stock's reproductive capacity is the primary consideration, then a minimum size limit (MSL) should be set above the SFM. Although a range of mathematical models is available for determining appropriate size limits (*e.g.* yield per recruit models), a simple yet conservative approach is to ensure that all individuals in the population have the opportunity to breed at least once before they are likely to be captured by the fishery (Chubb 2000). Given that female painted crayfish grow at 18 mm yr^{-1} (Figure 4.7a) when they attain SFM (78 mm CL), an appropriate MSL would be 96 mm CL. However, it is probably justifiable to increase the MSL to 100 mm CL, since this would simplify both compliance and enforcement of the proposed regulation. Importantly, implementation of a 96 or 100 mm CL MSL is unlikely to have a big, immediate impact on the fishery, because only a small proportion of the current catch is less than 100 mm CL (Figure 2.3). However, this regulation will act as a good insurance policy for (predicted) future increases in fishing effort and (or) a decline in the abundance of larger (>100 mm CL) crayfish (Chubb 2000; Walters and Martell 2004).

Growth rate of adult *P. versicolor* decreased with increasing size. This pattern of growth is typical of palinurids and usually results from a combination of increasing moult interval and decreasing growth increment (Mauchline 1977; Wahle and Fogarty 2006). For *P. versicolor*, growth increment was estimated to be in the range of 2−3 mm CL, but the magnitude of this increment did not decline with increasing body size for the range of sizes examined (Figure 4.5). *Prima facie*, this result is unusual, because it suggests that growth in *P. versicolor* is unlike that of other palinurids. However, it remains possible that growth increment in *P. versicolor* does decline with increasing size, but only until CL reaches *ca*. 90 mm (in which case any decline in growth increment would not have been detectable due to the limited size range of crayfish that were sampled in this study). Size-related reductions in growth increment may also be very small in *P. versicolor* – that is, too small to be detected using vernier calipers with a precision of ±0.5 mm.

Moult interval for larger crayfish (326 ± 31 d) was approximately double that for smaller crayfish (159 ± 18 d). Moreover, many of the larger crayfish did not moult during inter-census periods (Figure 4.6). Together, these results suggest that moult interval in *P. versicolor* increases with increasing size (and presumably increasing age), as it does in other palinurids (Mauchline 1977; Wahle and Fogarty 2006). Interestingly, only the very largest of crayfish (including those not recaptured) had macroscopic epiphytes growing on their exoskeleton. This observation suggests that moult intervals for these animals are protracted, and thus supports the notion that growth rate in *P. versicolor* is asymptotic.

The predicted lifetime growth trajectory of *P. versicolor* (Figure 4.8) was similar to that reported for other tropical west Pacific palinurids (*e.g. P. ornatus*, *Panulirus penicillatus*, *Panulirus longipes*). Indeed, the estimated values of L_∞ (144.7 mm) and K (0.27 yr^{-1}) were within the range reported for these other species (range: L_∞, 118−164 mm; K, 0.27−0.54 yr^{-1}) (Phillips *et al*. 1992; Pitcher 1993; Skewes *et al*. 1997). In contrast, temperate palinurids such as *J. edwardsii*, *P. cygnus* and *Palinurus gilchristi* attain a similar size (L_∞, 98−171 mm) but moult less often (<1 yr^{-1}) and grow markedly slower (K, 0.06−0.20 yr^{-1}) (Annala and Bycroft 1988; Phillips *et al*. 1992; Groeneveld 1997). Together, these results support the generalization that aquatic animals grow faster with decreasing latitude, probably due to the effects of temperature on metabolism (Belk and Houston 2002; Heibo *et al*. 2005).

It is apparent from the predicted von Bertalanffy growth trajectory that it takes *ca*. 3 yr for *P. versicolor* to attain sexual maturity (78−88 mm CL) and 10−12 yr to approach maximum size (Figure 4.8). The apparent longevity of other palinurids ranges from 10−14 yr (Phillips *et al*. 1983; Phillips *et al*. 1992; Pitcher 1993). Future research, perhaps using the morphological lipofuscin technique described by Sheehy (1990), will be needed to validate these predictions. With regard to the culture potential of *P. versicolor*, it would take *ca*. 2 yr for puerulus stage juveniles to reach marketable size (60−70 mm CL), assuming that growth in captivity is not slower than growth in the wild. This timeframe would not appear to preclude *P. versicolor* as a successful candidate for future aquaculture, especially when the monetary value of this species is considered.

This study is the first to characterize the lifetime growth trajectory of *P. versicolor*. It is also one of a very few to have characterized growth in a crustacean using tags of a type that resist ecdysis and that have no apparent effects on growth (see Woods and James 2003; Frisch and Hobbs 2006). This is significant given the degree to which conventional tag types can bias estimates of growth parameters (Rowe and Haedrich 2001; Dubula *et al.* 2005).

In conclusion, the data presented here will provide a useful starting point for the management of *P. versicolor* − an important fishery resource on the GBR. Firstly, implementation of a minimum legal size of 100 mm CL will ensure that all female crayfish have the potential to breed before recruitment to the fishery. Secondly, estimates of growth parameters (L_∞, K and t_0) can be incorporated into yield models, thereby improving the accuracy of yield assessments. These advances are important given the current paucity of quantitatively-derived population data for *P. versicolor*. Future work should seek to identify spatial differences in growth and reproductive characteristics of GBR sub-populations, as well as the destination(s) of migrating females.

CHAPTER 5: Demography

Abstract

Mark-recapture techniques and a length-based method were used to quantify demographic parameters (abundance, mortality and immigration) of painted crayfish (*Panulirus versicolor*) at Northwest Island, an offshore coral cay. The local population was estimated to be small in size (1400 ± 185 individuals) and sparsely distributed (1.3 ± 0.2 individuals ha^{-1}), even by tropical Pacific standards. Despite being exposed to potentially high fishing pressure, the estimated mortality rate was low (0.28 ± 0.04 yr^{-1}, mark-recapture method; 0.25 ± 0.08 yr^{-1}, length-based method), perhaps because the study was conducted away from the most frequently fished parts of the reef. With respect to immigration, preliminary observations suggest that arrival ('recruitment') of sub-adult individuals to Northwest Island may be episodic. Also, the virtual absence of juveniles at Northwest Island and their presence at some inshore reefs suggests that this species may undergo an ontogenetic habitat shift, as do most of its congeners. Lastly, it is apparent that survival of *P. versicolor* is minimally influenced by partial loss of legs and antennae – an important consideration for any mark-recapture program in which subjects are occasionally injured.

5.1 Introduction

Demography is the study of numbers of individuals in a population and their variation over time. The most important demographic parameters are generally considered to be abundance, recruitment and mortality, since these provide the most useful information with respect to conservation and management of exploited species (King 1995; Walters and Martell 2004).

The demography of spiny lobsters that support large commercial fisheries (*e.g. Panulirus argus*, *Panulirus cygnus* and *Jasus edwardsii*) has been well defined and is amply reported in the literature (*e.g.* Morgan 1974; Lozano-Alvarez *et al.* 1991; Forcucci *et al.* 1994; Booth 2000; Hunt 2000; Phillips *et al.* 2000; Gonzalez-Yanez *et al.* 2006). The summation of this information has led to the development of a generalised model of palinurid life history (see Kanciruk 1980; Lipcius and Eggleston 2000; Butler *et al.* 2006). However, there is no adequate ecological or demographic description of any tropical Pacific palinurid species, and in many cases the most basic information is lacking (Pitcher 1993; Munro 2000). Consequently, the generality of the model with regard to tropical Pacific species remains unclear.

Because it is not possible to determine the age of palinurids, many of the quantitative methods employed in studies of fish populations cannot be used. Thus, parameters such as mortality must be estimated indirectly using growth and (or) length-frequency data (Morgan 1980). For example, mortality of spiny lobsters is often estimated by length-converted catch curve (LCCC) analysis, which involves conversion of length frequencies to age frequencies using von Bertalanffy growth parameters (Pauly 1983).

Another useful method for estimating demographic parameters of spiny lobster populations is multiple mark-recapture. In a typical study, a portion of the population is captured on each of several occasions (at least three), unmarked individuals are given a unique mark, marked individuals are noted, and then all individuals are released (*e.g*. Forcucci *et al*. 1994; Sharp *et al*. 1997). Estimates of demographic parameters are subsequently derived from the number and proportion of marked *versus* unmarked individuals that are captured in successive samples (Seber 1973). Although several mathematical models are available for analysing the data, the Jolly-Seber model is particularly useful because it can simultaneously estimate population size, survival (or mortality) and recruitment (or immigration). Furthermore, it allows each of these parameters to vary with time (Krebs 1999).

The first goal of this chapter was to describe the demography of painted crayfish (*Panulirus versicolor*) at Northwest Island (Great Barrier Reef; GBR) using a Jolly-Seber, multiple mark-recapture model. For the purpose of comparison, mortality was also quantified using LCCC analysis. In both cases, estimates were based on adult (>90 mm CL) individuals, since juveniles were virtually absent from the study site (see section 4.2.4). The second goal of this chapter was to find where the juveniles live and thus elucidate the life history of this species with respect to ontogenetic shifts in habitat use.

5.2 Materials and methods

5.2.1 Mark-recapture program

Animals used in this study were the same as those described in Chapter 3. As such, the reader should consult section 3.2.1 for details regarding the capture method, tagging technique and census periods. Briefly, a 60 ha section of coral reef (1.5 km of reef edge) at Northwest Island was censused on six occasions between December 2003 and December 2006 and all crayfish encountered were captured, tagged (with elastomer implants), measured (carapace length; CL) and released.

The total area of coral reef at Northwest Island was estimated to be 1100 ha. Approximately 10% of this is designated 'no take' marine reserve, with the remaining 90% 'open' to various forms of fishing. A campground on the island supports up to 150 people, and small catches of *P. versicolor* are regularly made by local fishers (Author's personal observation). Although the study site was located outside the reserve, it was anticipated to receive little or no fishing pressure. This is because the study site is difficult to access due to wave exposure and shallow water.

5.2.2 Jolly-Seber analysis

Formulae used to calculate population size, survival and immigration are provided in Appendix 1 and follow the form of Krebs (1999). As recommended by Seber (1973), a correction factor was included in the analysis to rectify bias in small samples (Appendix 1). To enable a comparison with LCCC results, finite survival rates (Φ_t) were converted to annualised instantaneous mortality rates (Z) using the equation:

$$Z = -\log_e(\Phi_t^2)$$

where the '^2' represents a conversion from bi-annual to annual rate. The overall annual mortality rate for the three-year study was calculated as the arithmetic mean of the annualised mortality rates for each census (Krebs 1999).

The assumptions of the Jolly-Seber model are that (1) sampling time is negligible relative to sampling interval, (2) tags are not lost or overlooked, (3) every tagged individual has the same probability of survival, and (4) every individual has the same probability of being captured, regardless of whether it is tagged or not (Krebs 1999). Given the sampling design used in this study, as well as the characteristics of elastomer tags (see Woods and James 2003; Frisch and Hobbs 2006), it was unlikely that assumptions one or two were violated. Injury was considered to be the most likely factor to influence survival of tagged crayfish (Davis 1981; Parsons and Eggleston 2005). Thus, assumption three was evaluated by categorising the condition of each crayfish into one of the following groups: ‘uninjured’, ‘minimally injured’ (missing 1−2 legs), or ‘moderately injured’ (missing ≥3 legs or 1–2 antennae). If injury affects survival, injured animals would be less likely to be recaptured than uninjured animals. Hence, the proportions of recaptured animals in each of the three groups were compared using a χ^2 homogeneity test (Zar 1999). With respect to assumption four, the likelihood of equal catchability was assessed using Leslie’s test (Krebs 1999).

5.2.3 Length-converted catch curve analysis

The CL of each crayfish was assigned to a 5 mm length class in order to construct a length-frequency distribution. The relative age of each length class was estimated using the inverse of the von Bertalanffy growth equation:

$$t = (-1/K) \times \log_e(1 - L_t/L_\infty)$$

where $K = 0.27$ and $L_\infty = 144.7$ (from Figure 4.8). The time taken for the species to grow through a particular length class (Δt) was calculated as the difference in relative ages between two adjacent length classes. Next, the natural logarithms of the frequency of each length class divided by the change in age [$\log_e(\text{frequency}/\Delta t)$] were plotted against mean relative age, t. Lastly, a regression line was fitted to the data, excluding length classes with small sample sizes ($n < 5$) or that exceeded L_∞ (King 1995). Regression parameters were derived using SPSS computer software (SPSS, Chicago, U.S.A.).

5.2.4 Ontogenetic shifts in habitat use

For most palinurid species studied to date, settlement occurs in shallow inshore areas such as rocky reefs and seagrass beds (Butler and Herrnkind 2000). Furthermore, juveniles normally remain in these habitats for the first 1–2 yr of life (Butler *et al*. 2006). With this in mind, the obvious place to search for juvenile painted crayfish was inshore areas of the Queensland coast. In December 2004, searches were conducted at Facing, Humpy and Barren Islands, which are approximately 3, 10 and 20 km (respectively) from the mainland coast near the city of Gladstone (Figure 1.2). In June 2007, searches were conducted at Hinchinbrook Island, Orpheus Island and Pandora Reef, which are 1, 8 and 12 km (respectively) from the mainland coast near the city of Townsville (Figure 2.1). The habitat in these locations varied from algal-dominated (*Sargassum* sp.) rocky reef to well developed coral reef. One SCUBA dive (*ca*. 1 hr in duration; 1−8 m in depth) was conducted at each location and all types of microhabitat (*e.g*. rubble ramparts, rock crevices, coral caves) were searched thoroughly. When a crayfish was encountered, its size (CL) was estimated visually. Where possible, a flexible rule was held next to each crayfish, thereby reducing the potential for bias.

5.3 Results

5.3.1 Jolly-Seber analysis

Eighty-five crayfish were tagged and released between December 2003 and December 2005. Eighteen crayfish (21%) were minimally injured and 15 crayfish (18%) were moderately injured. The latter group included one individual that had lost both antennae, and another individual that had lost seven legs. Both of these animals were recaptured after 12 and 36 months (respectively) and both had regenerated their missing appendages. Uninjured, minimally injured and moderately injured crayfish were recaptured in similar proportions (χ^2 test, $\chi^2_2 = 0.63$, $p > 0.5$; Figure 5.1). Thus, injury did not affect crayfish survival and assumption three of the Jolly-Seber model was probably satisfied. Similarly, the catchability of tagged crayfish was not significantly different (Leslie's test, $\chi^2_5 = 6.8$, $p > 0.1$), thereby satisfying the fourth assumption of the Jolly-Seber model.

Seventeen to 50 crayfish were captured and 8−21 crayfish were recaptured during each of the six censuses (Table 5.1). The proportion of marked animals in the population increased throughout the study and ranged from 16% during the second census to 82% during the final census. According to the Jolly-Seber model, there was a mean of 76 ± 10 painted crayfish in the study area (60 ha) during each census (June 2004 to December 2005), which is equivalent to a density of 1.3 ± 0.2 individuals ha^{-1} (Table 5.2). Assuming a similar density of crayfish on other parts of the reef, the total abundance of crayfish at Northwest Island was estimated to be 1400 ± 185 individuals. From June 2004 to December 2005, the mean instantaneous mortality rate (Z) was 0.28 ± 0.04 yr^{-1} and the mean number of immigrants to the study area was 3 yr^{-1} (Table 5.2).

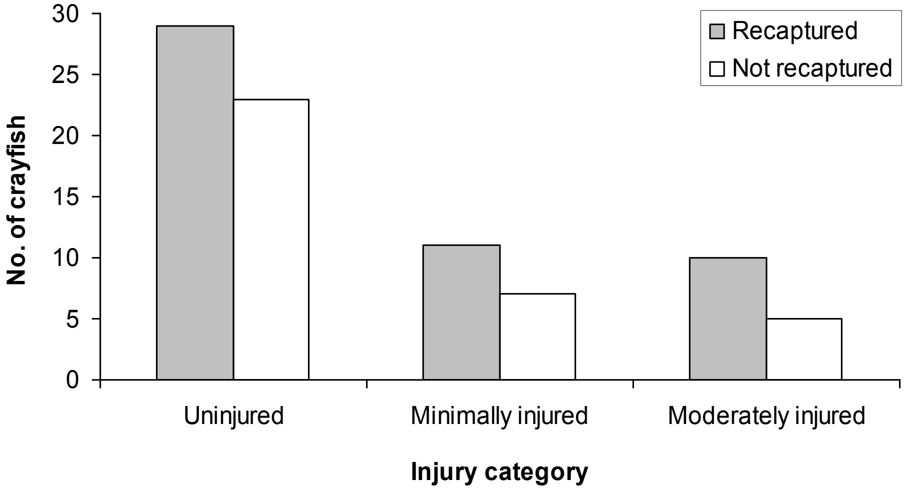

Figure 5.1 The effect of injury on the number of *Panulirus versicolor* that were subsequently recaptured after 6–36 months. Differences between categories were not statistically significant ($p > 0.5$). See section 5.2.2 for definitions of injury categories.

Table 5.1

Mark-recapture data for *Panulirus versicolor* at Northwest Island (data are cast in a 'Method B' table, as per Krebs 1999).

	Time of capture					
Time of last capture	Dec. 2003	June 2004	Dec. 2004	June 2005	Dec. 2005	Dec. 2006
Dec. 2003		8	1	3	2	0
June 2004			20	6	3	2
Dec. 2004				12	6	1
June 2005					7	8
Dec. 2005						7
Total marked	0	8	21	21	18	18
Total unmarked	17	42	11	11	4	4
Total caught	17	50	32	32	22	22

Table 5.2

Jolly-Seber population estimates (± SE) for *Panulirus versicolor* at Northwest Island

Time[a]	Population size[b]	Density (ha^{-1})	Mortality rate (*Z*) (yr^{-1})	Immigration (yr^{-1})
June 2004	100 ± 31	1.7 ± 0.5	-0.07 ± 0.08[c]	–
Dec. 2004	71 ± 11	1.2 ± 0.2	0.46 ± 0.04	-16[c]
June 2005	75 ± 14	1.3 ± 0.2	0.32 ± 0.08	28
Dec. 2005	60 ± 18	1.0 ± 0.3	0.41 ± 0.13	-2[c]
Mean	76 ± 10	1.3 ± 0.2	0.28 ± 0.18	3

[a] Estimates for December 2003 and December 2006 were not possible
[b] Per 60 ha (the size of the study area)
[c] Negative estimates were artefacts of sampling error (see Krebs 1999)

5.3.2 Length-converted catch curve analysis

The mean size of males (124 ± 2 mm CL) and females (125 ± 2 mm CL) at Northwest Island was not significantly different (*t* test, $t_{83} = 0.37$, $p = 0.71$). Consequently, the data for each group were pooled for analysis. The resulting length-frequency distribution was bi-modal (mode 1 = 107.5−112.5 mm CL, mode 2 = 132.5−137.5 mm CL; Figure 5.2). There was a significant relationship between $\log_e(\text{frequency}/\Delta t)$ and mean relative age (ANOVA, $F_{1,8} = 10.4$, $p = 0.012$; Figure 5.3). The slope of the regression line, which is the estimated mortality rate (*Z*), was 0.25 ± 0.08 yr^{-1} and the co-efficient of determination (r^2) was 0.56.

5.3.3 Ontogenetic shifts in habitat use

No painted crayfish were found at Facing, Humpy or Barren Islands. A total of 16 painted crayfish were observed at Hinchinbrook Island, Orpheus Island and Pandora reef. In terms of body size, the median and range of these crayfish were 65 mm CL and 20−100 mm CL, respectively. All crayfish were observed in holes or crevices in rock or coral, each scaled to the size of the resident crayfish.

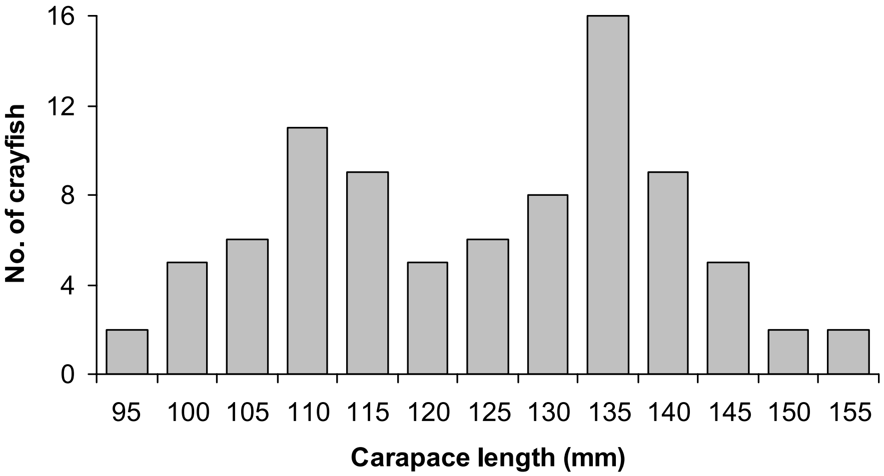

Figure 5.2 Length-frequency distribution of *Panulirus versicolor* that were captured at Northwest Island between December 2003 and December 2006. The *x*-axis labels are size-class midpoints.

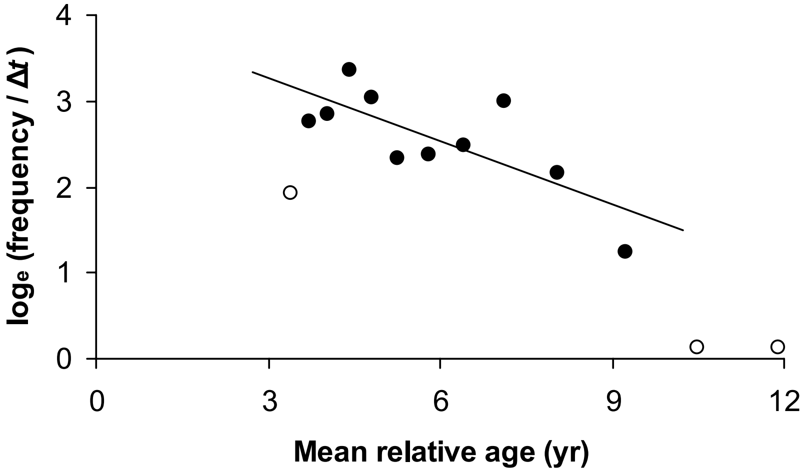

Figure 5.3 Length-converted catch curve (LCCC) for *Panulirus versicolor* at Northwest Island. Data included in the regression analysis are shown as *solid circles*. The instantaneous mortality rate (*Z*) estimated from the slope of the line regression line is 0.25 yr^{-1}.

5.4 Discussion

The total number of painted crayfish at Northwest Island was estimated to be 1400 ± 185, which is equivalent to 1.3 ± 0.2 individuals per hectare of shallow reef habitat, or 51 ± 8 individuals per kilometre of reef edge. Other estimates of palinurid density in the tropical west Pacific are 10 individuals per hectare of reef habitat (*Panulirus ornatus*, Pitcher *et al*. 1992) and 95 individuals per kilometre of reef edge (*Panulirus penicillatus*, Ebert and Ford 1986). The density of *P. versicolor* at Northwest Island is thus very low, even by tropical Pacific standards. Consequently, the local stock can only be expected to sustain relatively light fishing pressure.

Jolly-Seber and LCCC estimates of (instantaneous) total mortality rate (Z) for *P. versicolor* were 0.28 ± 0.04 and 0.25 ± 0.08 yr^{-1}, respectively. In finite terms, *ca*. 22−24% of the population died or was removed during each year of the study. This is considerably less than for exploited populations of other palinurids, which typically have Z values of 0.4−1.6 yr^{-1} (33−80% in finite terms) depending on the degree of exploitation (Morgan 1980; Pitcher 1993; Muller *et al*. 1997; Pitcher *et al*. 1997). In general, models for estimating mortality rates are less robust than models used to estimate other population parameters such as growth (King 1995). Consequently, fishery scientists are often uneasy about their estimates of mortality rate, even in the most intensively studied fisheries (Jennings *et al*. 2001). With respect to the present estimates, however, some level of confidence is gained by the fact that both Jolly-Seber and LCCC estimates were similar in magnitude, despite being derived independently.

In an exploited population, total mortality rate (*Z*) consists of contributions of both fishing mortality (*F*) and natural mortality (*M*). Separating *F* from *M* generally requires extensive catch and effort records (Morgan 1980), which was beyond the scope of this study. However, it is noteworthy that no fishing was observed within the 60 ha study area during the 70+ days that the author was in attendance (instead, fishing occurred at other, more accessible areas of Northwest Island). This observation, in combination with the small home-range of *P. versicolor* (see Chapter 6), suggests that *F* was probably negligible for crayfish in the study area. The length-frequency distribution of the population provides further support for this notion; modal size classes were 107.5–112.5 and 132.5−137.5 mm CL, and 33% of crayfish were >135 mm CL (Figure 5.2). In comparison, *P. versicolor* from an exploited (spearfished) population in Palau (Micronesia) had a modal size class of 95−105 mm CL, and 100% of the catch was ≤135 mm CL (MacDonald 1982). Furthermore, 100% of *P. versicolor* in samples collected from Western Australia and India were ≤120 mm CL (George and Morgan 1979; Kuthalingam *et al*. 1980).

If, as hypothesised, *F* was negligible, then *Z* can be assumed to approximate *M*. Only two estimates of *M* are currently available for any tropical west Pacific palinurid; these are 0.42 yr^{-1} for *P. penicillatus* at Marshall Islands (males and females combined; Ebert and Ford 1986) and 0.69 yr^{-1} for *P. ornatus* at Torres Strait (Pitcher *et al*. 1997). Given that *P. penicillatus*, *P. ornatus* and *P. versicolor* have similar growth parameters (*cf*. Ebert and Ford 1986; Skewes *et al*. 1997; Frisch 2007a), and that *M* results very largely from predation (Kanciruk 1980; Morgan 1980), it may be inferred that estimates of '*M*' reflect the relative intensity of predation on the three species. Factors that influence predation rates and that are likely to vary among locations include the quality and quantity of shelter (dens), the relative abundance of conspecifics, and of course, the density of predators (Smith and Herrnkind 1992; Mintz *et al*. 1994).

In general, tropical palinurids spawn and recruit continuously, with the result that length-frequency distributions tend to be unimodal (Pitcher 1993). It is therefore unusual that the length-frequency distribution of *P. versicolor* at Northwest Island was bimodal. This result was neither an artefact of biased sampling, since adult crayfish are equally vulnerably to hand-capture, nor sex-related, because males and females were similar in size (CL) and were homogeneously distributed among size classes. As such, the only reasonable explanation is that the population contained one or two unusually strong cohorts, as is common among temperate palinurids (Caputi *et al*. 2003; Butler *et al*. 2006). Interestingly, immigration of *P. versicolor* to the study area varied considerably among censuses (Table 5.2). In this context, immigration may actually represent arrival (or recruitment) of sub-adult individuals to Northwest Island (see below).

If indeed ‘recruitment’ is episodic, then the LCCC-derived estimate of mortality may be biased, since LCCC analyses assume a stable size structure (Pauly 1983). However, it is unclear what effect any such bias may have had on the estimated mortality rate because it is not known whether the first, second or both modal size classes were over-represented. In any case, the LCCC mortality estimate presented here should be interpreted with caution.

It is interesting that injured crayfish were recaptured in the same proportion as uninjured crayfish because this suggests that survival was independent of injury. Previously, Parsons and Eggleston (2005) found a three fold difference in the mean survival rates of injured (missing one antenna and two legs) and uninjured *P. argus* that were tethered in the wild. They postulated that the lower survival rate of injured individuals was due to (1) enhanced prey detection by predators due to release of body fluids (*e.g*. blood), (2) impaired ability to escape from, or defend against, predators, and (3) loss of co-operative group defence due to the tendency of conspecifics to avoid injured animals. It is also plausible that a reduced complement of walking legs impairs foraging efficiency, with the result that injured individuals are predisposed to starvation or forced to take greater risks to obtain food. Thus, it is difficult to explain why injured and uninjured crayfish were recaptured in similar proportions during the present study. Nonetheless, it is clear that painted crayfish are generally resilient to occasional loss of legs and antennae – a paramount consideration for any mark-recapture program in which subjects are sometimes injured.

Most palinurid species have life history stages that can be described as triphasic: oceanic planktonic larva, inshore benthic juvenile, offshore benthic adult (Kanciruk 1980; Butler *et al*. 2006). Preliminary observations at inshore reefs near Townsville suggest that *P. versicolor* conforms to this generalised model. Juvenile crayfish as small as 20 mm CL were found at Hinchinbrook Island, Orpheus Island and Pandora Reef. Moreover, the median size of crayfish at these locations (all of which are 'no take' marine reserves) was only 65 mm CL (*i.e.* well under the estimated size at first maturity; 78−88 mm CL). Thus, it is conceivable that individuals recruit to inshore reefs and then migrate offshore as they approach maturity. However, it seems that recruitment is site-specific, since no juvenile crayfish were observed at inshore reefs near Gladstone. Clearly, much more work needs to be done to fully understand the life history of this species.

In summary, this study has demonstrated that painted crayfish are not an abundant species at Northwest Island and thus can only be expected to sustain relatively light fishing pressure. Although catches of *P. versicolor* are common at this location, relatively few individuals appear to be removed by fishing (at least within the study area) because the mortality rate of the population was very low in comparison to that of exploited palinurids at other locations. With respect to the life history of *P. versicolor*, preliminary observations suggest that individuals may undergo an ontogenetic habitat shift, and that arrival (‘recruitment’) of sub-adult individuals to offshore reefs may be episodic. Lastly, it is apparent that *P. versicolor* is resilient to loss of legs and antennae – an important consideration for any mark-recapture program that occasionally injures its subjects.

CHAPTER 6: Movement patterns

Abstract

Defining the movement patterns of an exploited species is an important component of fisheries management, particularly with respect to the design of marine reserves. However, movement data obtained *via* mark-capture programs are often influenced by artefacts such as displacement, tag-loss and tag-induced injury. To overcome these problems, an unconventional approach was employed to investigate the movements of painted crayfish, *Panulirus versicolor*, at Northwest Island. Eighty-nine adult crayfish were captured by hand and subsequently tagged internally (with elastomer) and externally (with plastic zip-ties), thereby enabling both short- (1−10 d) and long-term (6−36 months) observations. After 6−36 months, 49 crayfish were recaptured within 500 m of their original den, indicating a high level of site-fidelity for this species. Short-term observations revealed that individuals moved frequently to and from nearby dens, and that male crayfish typically moved further than female crayfish. It was hypothesised that male crayfish move about their home range more actively, perhaps to seek mating opportunities or to defend resources. With respect to the management of this species, it was concluded that relatively small ‘no take’ marine reserves would provide a high level of protection for resident individuals of this species.

6.1 Introduction

Many species of palinurids are known to engage in temporally organised and spatially orientated movements such as migration, homing and nomadism (Herrnkind 1980; Childress and Jury 2006). An understanding of these movements is valuable with regard to fisheries management and conservation. For example, movement patterns can influence the effectiveness of marine reserves, since species that roam widely are more likely to cross reserve boundaries and thus be subjected to fishing (Roberts and Polunin 1991; Kelly and MacDiarmid 2003). Also, movements can influence estimates of population size – a crucial component of stock assessment and yield analysis (Seber 1973; King 1995).

The most common method for estimating movement patterns of spiny lobsters is *via* mark-recapture (Herrnkind 1980). However, conventional crustacean tags (*e.g.* T-bar, sphyrion and streamer tags) have significant annual loss-rates and can cause entanglement and internal injury – factors that are likely to bias patterns of movement (Scarrat 1970; Ennis 1986; Melville-Smith and Chubb 1997; Rowe and Haedrich 2001; McPherson 2002). In contrast, internal elastomer implants are small, flexible, visually discrete, and resistant to ecdysis (Woods and James 2003; Frisch and Hobbs 2006). This allows tagged animals to be tracked for long-term periods without bias resulting from physical hindrance or tag-induced predation (Bergman *et al*. 1992).

Mark-recapture investigations of movement in palinurids often utilise commercial fishing operations to obtain experimental animals (*e.g.* Phillips 1983; Moore and MacFarlane 1984;

Bell *et al*. 1987). Whilst providing a number of substantial benefits, this practice has one distinct drawback: many individuals may be displaced from their capture location prior to release. Aside from dissipating fine-scale movement information, displacement may also affect subsequent behaviour and movement (*e.g.* due to disorientation) (Chittleborough 1974). At the other end of the spectrum, studies that involve direct observations are generally too short in duration to detect seasonal or annual movement patterns (*e.g.* Yoshimura and Yamakawa 1988; Acosta 1999).

The goal of this chapter was to describe the movement patterns of painted crayfish (*Panulirus versicolor*) using mark-recapture techniques. Unlike other studies, however, all individuals were captured by hand (to avoid displacement) and recaptures (or resightings) were made over both short-term (daily) and long-term (6−24 months) periods. This was achieved by the use of two types of tag, one external and one internal.

6.2 Materials and methods

6.2.1 Study site

For logistical reasons, observations were confined to an area of 60 ha adjacent to the reef crest of Northwest Island. This area was relatively homogeneous, consisting of scattered coral outcrops with interspersed sand patches (locally known as a ‘bommie’ field). There were no obvious barriers to movement within or across the boundaries of the study area, although nearby rubble barrens (beyond the reef edge) and tracts of sand (in the lagoon) were devoid of suitable dens. Approximately 500 m from the study area was a ‘no take’ marine reserve and all three habitat types (*i.e.* bommie field, sandy lagoon and rubble barrens) were contiguous across both areas. Before commencement of the tagging program, the study area was systematically searched to locate all useable dens. The positions of these dens were recorded using a Global Positioning System (GPS) to thereafter enable rapid surveys of the study area.

6.2.2 Capture and tagging

Adult crayfish were captured by hand (while using SCUBA) and transferred to a water-filled tank onboard a nearby support vessel. The gender of each crayfish was determined using externally dimorphic features (Phillips *et al*., 1980) and carapace length (CL) was measured using vernier calipers (± 0.5 mm). Next, crayfish were uniquely tagged on one or both antennae with colour-coded, plastic zip-ties (CT200, Cabac, Silverwater, Australia). This enabled individuals to be identified (resighted) over short-term periods (1−10 d) without disturbance. To facilitate long-term (6−36 months) observations, crayfish were also marked with moult-resistant elastomer implants (Northwest Marine Technology, Shaw Island, U.S.A.). A complete description of the tagging technique is provided by Frisch and Hobbs (2006). The entire tag-and-measure process was completed in approximately 5 min after which each crayfish was manually returned to its den.

The study site was searched daily for ten consecutive days on six occasions: December 2003, June 2004, December 2004, June 2005, December 2005 and December 2006. All newly-encountered crayfish were tagged and released. Plastic zip-ties were replaced on previously captured (*i.e.* elastomer-tagged) crayfish that had moulted during the inter-census period. The distance travelled by each crayfish was calculated trigonometrically using GPS co-ordinates.

6.2.3 Data analyses

Sex-specific recapture rates were compared using a χ^2 test, while the nightly and annual movement distances of males and females were compared using a *t* test (Zar 1999). The relationship between distance travelled and time-at-liberty was assessed using one-way ANOVA (Zar 1999). The assumptions for each test were checked *a priori* and, where appropriate, group variances were stabilised by transformation [$\sqrt{(x + 0.5)}$]. Probability values were determined using SPSS computer software (SPSS, Chicago, U.S.A.).

6.3 Results

Eighty-nine adult *P. versicolor* were tagged and released between December 2003 and December 2006. Of these, 40 were male (mean size 122 ± 3 mm CL) and 49 were female (mean size 125 ± 2 mm CL). Sixty-two of these crayfish (71%) were resighted or recaptured 1−1,100 d after initial capture, with each crayfish observed an average of 4.3 times. In all, 123 movements were recorded, most of which involved short (but repeated) excursions to and from nearby dens. Movements to far dens (*i.e.* >500 m away) were rare (Figure 6.1).

6.3.1 Short-term (1−10 d) movements

There were 122 short-term resightings of 50 crayfish. Thirty-eight (76%) of these individuals moved frequently among nearby dens. The remaining twelve individuals were observed only at the den in which they were initially captured. Male crayfish generally moved further than female crayfish (Figure 6.2). Mean nightly movement distances for males (34 ± 6 m) and females (17 ± 3 m) were significantly different (*t* test, $t_{48} = 2.0$, $p = 0.049$). The largest single movement observed on any one night was 459 m by a male.

6.3.2 Long-term (6−24 months) movements

Fifty crayfish (26 males and 24 females) were recaptured after 6−36 months. The recapture rate for male and female crayfish (70% *versus* 50%, respectively) was not significantly different ($\chi^2_1 = 1.8$, $p > 0.10$). Thirty-one percent of crayfish were recaptured at their original den (although some had occupied other dens for short-term periods), while 53% of crayfish were recaptured within 100 m of their original den (Figure 6.3). Mean annual distances travelled for males and females (196 ± 31 m y^{-1} and 124 ± 30 m y^{-1}, respectively) were not significantly different (*t* test, $t_{48} = 1.7$, $p = 0.10$). Distance travelled was not related to time at liberty for individuals recaptured after 6−36 months (ANOVA, $F_{3,46} = 0.6$, $p = 0.6$; Figure 6.4).

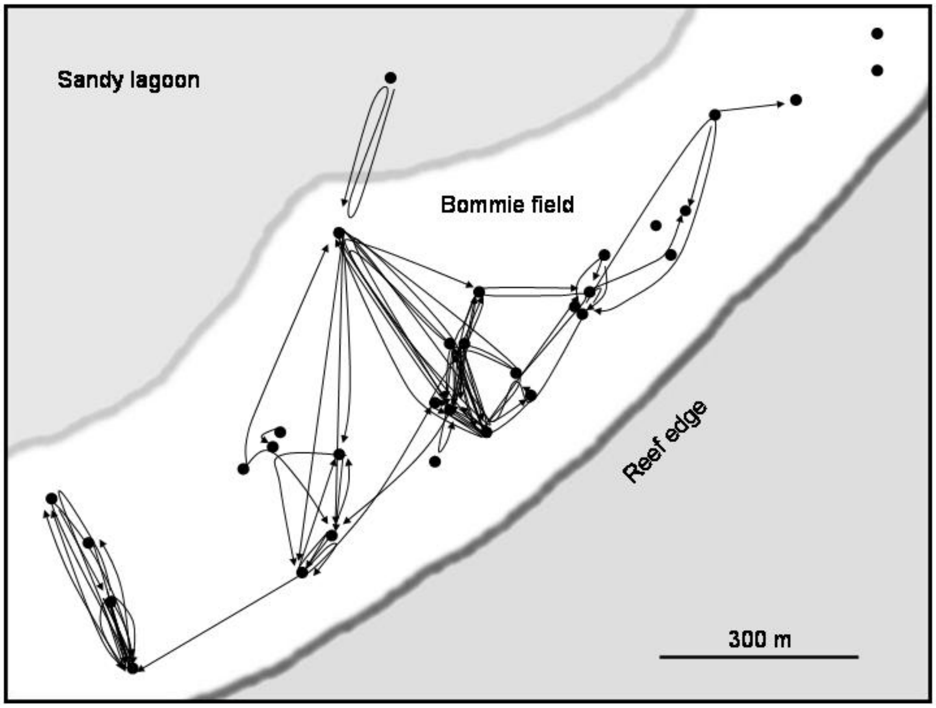

Figure 6.1 Recorded movements of *Panulirus versicolor* at Northwest Island between December 2003 and December 2006. Each *line* represents the track of one individual and *arrowheads* depict the direction of movement. Movements less than 25 m are not shown due to scale limitations. Total search area was 60 ha.

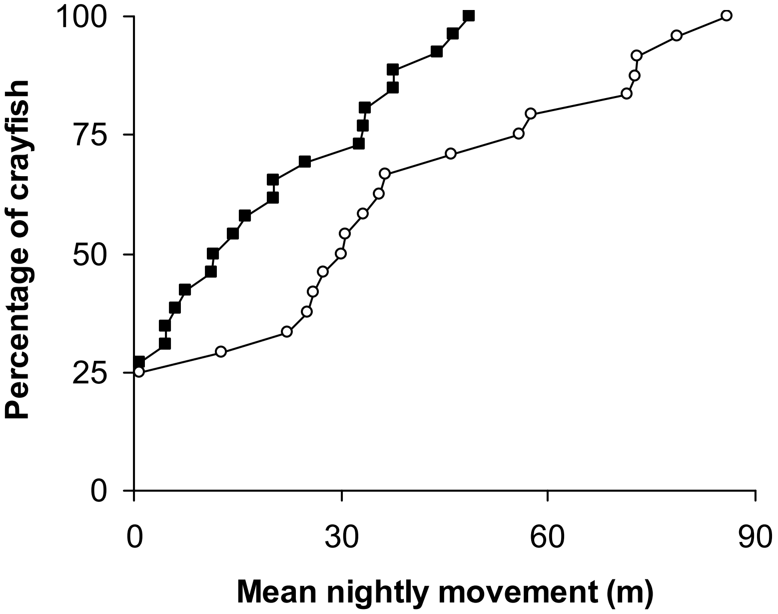

Figure 6.2 Cumulative distribution of mean nightly movements of male (*white circles*) and female (*black squares*) *Panulirus versicolor* at Northwest Island. Mean movements of individual crayfish were calculated over periods of 1−9 days.

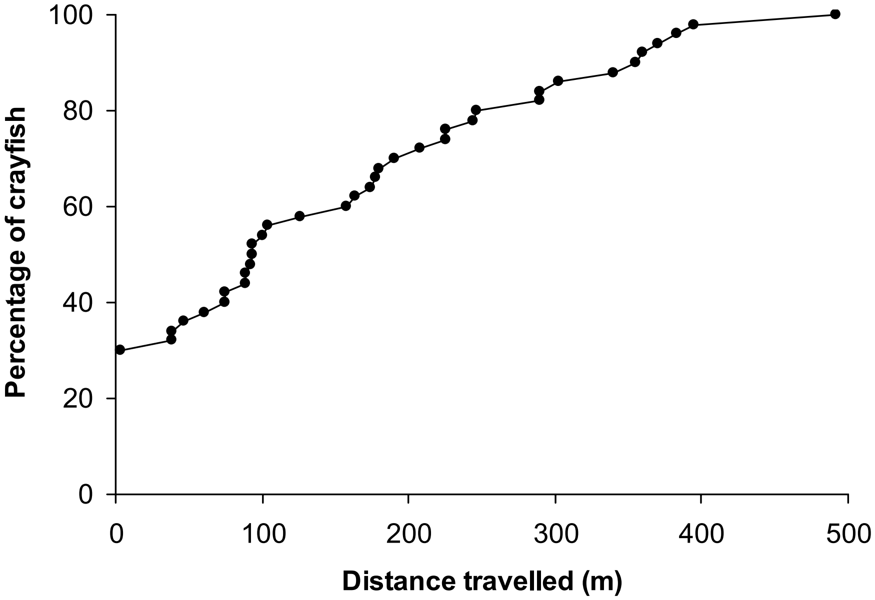

Figure 6.3 Cumulative distribution of the distance between first release and last recapture of *Panulirus versicolor* at Northwest Island (n = 50). All individuals were at liberty for 6−36 months.

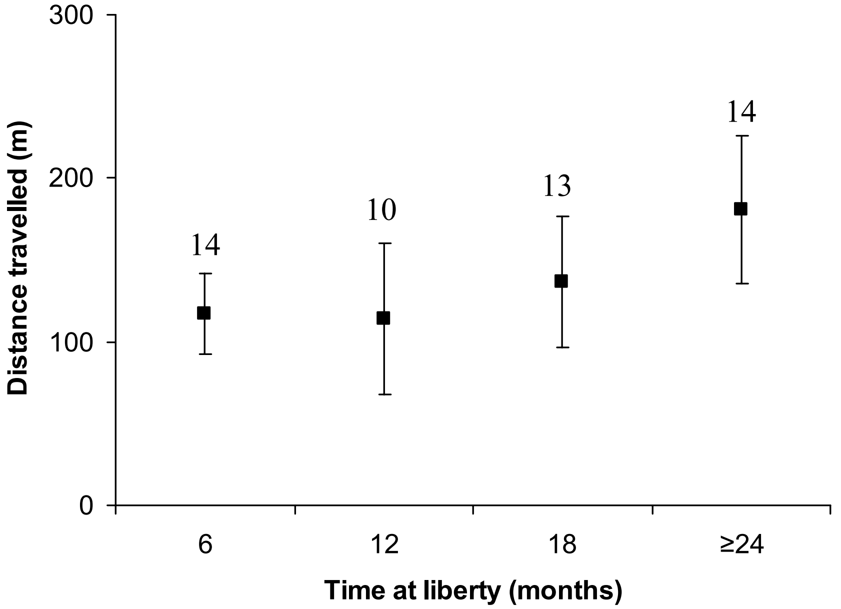

Figure 6.4 Mean distance travelled (± SE) by tagged *Panulirus versicolor* during the period between first release and last recapture (*n.b.* short-term resightings are not included). Differences between groups were not statistically significant (p = 0.6). Sample sizes are shown above each group.

6.4 Discussion

This study investigated the movement patterns of painted crayfish over both short- and long-term periods. Unlike other studies however, the confounding effects of tag-loss and displacement were avoided by (1) using highly-resistant elastomer implants, and (2) manually returning tagged crayfish to their dens. The results presented here are thus likely to reflect natural movements, rather than artefacts of capture procedures or tagging anomalies.

Daily observations of tagged crayfish indicate that *P. versicolor* has the potential to move considerable distances in short-term periods (up to 459 m d^{-1}). This is not unlike other palinurids (*e.g*. *Panulirus cygnus*, Phillips 1983; *Panulirus ornatus*, Moore and MacFarlane 1984; *Jasus edwardsii*, MacDiarmid *et al*. 1991; *Panulirus argus*, Lozano-Alvarez *et al*. 2003), and thus supports the notion that this group of animals are highly mobile. Despite this mobility, a large proportion (57%) of tagged crayfish were found at or close to the den in which they were originally captured, even after 6−36 months. This result suggests either that tagged individuals did not leave the study area, or that they returned 'home' after movements abroad. Given the consistently high recapture rate of tagged animals during successive censuses, the former explanation seems the most parsimonious. Continuous occupation of small patch reefs has been observed in other species (*e.g*. *P. cygnus*, Chittleborough 1974; *P. argus*, see Herrnkind 1980 and references therein; *J. edwardsii*, Kelly and MacDiarmid 2003), thus suggesting that site-fidelity is common among palinurids for at least part of their life history.

The home range of an animal is defined as the area that it utilises but does not necessarily defend, and is most often quantified using the polygon method (Chittleborough 1974; Alcock 1998). The home range of *P. versicolor* appears to be relatively small, perhaps 200−300 m in diameter (Figure 6.1). This finding suggests that relatively small 'no take' marine reserves could provide a high level of protection for resident crayfish (assuming the behaviour of *P. versicolor* is comparable in different areas). This has particular relevance to the reef at Northwest Island, since the marine reserve at this location is only 2.5 km wide where it intersects the bommie field. Even if adjacent areas were subject to intense fishing pressure, this reserve would act as a suitable refuge for *P. versicolor*, since relatively few individuals are likely to be captured as a result of cross-border movements. An adequate 'no-take' reserve would appear to be especially important for the protection of *P. versicolor* at Northwest Island, because the population at this location is relatively small (*i.e.* 1400 ± 185 individuals; see Chapter 5) and thus easily overfished.

Sex-specific movements have been recorded for a number of palinurid species (reviewed by Herrnkind 1980; Lipcius and Eggleston 2000). In some cases, these movements formed part of a long-distance migration that lasted several months (*e.g. P. ornatus*, Moore and MacFarlane 1984). In other cases however, sex-specific movements occurred over much smaller scales, both in time and space. For example, MacDiarmid *et al*. (1991) found that most females of *J. edwardsii* moved to nearby dens at night, while males either stayed within their dens or moved to nearby dens during the day or night. In the present study, male crayfish moved twice as far as female crayfish (on a nightly basis) and did so without leaving the putative home range. This suggests that male crayfish move about their home range more actively than females, perhaps to seek mating opportunities or to defend resources (*e.g.* dens or food). Although short-term, male-biased movements have been observed among many other animals (Alcock 1998), this type of behaviour has not been recorded previously for any palinurid.

Although the overall recapture rates of male and female crayfish (70% and 50%, respectively) were not significantly different, most of the crayfish recaptured in December (summer) were male, whereas most of the crayfish recaptured in June (winter) were female. One explanation is that some female crayfish emigrated to other habitats or reefs during summer, presumably to spawn. Indeed, reproductive migrations are common among palinurids and presumably serve to increase the survival of their propagules (see Chapter 4). If female crayfish do move long distances, 'no take' reserves should be used in combination with other management controls (*e.g.* 'closed' seasons). This would facilitate the protection of both resident and migrating crayfish without the need for exceedingly large 'no take' areas. Indeed, many of the world's spiny lobster fisheries employ a combination of catch limits, gear restrictions and 'closed' seasons, as well as 'no take' reserves (Annala and Sullivan 1997; Lipcius and Eggleston 2000).

It is important to note that long distance movements by tagged *P. versicolor* were not detectable in this study due to the limited size of the search area. As a result, the long-term movement patterns reported here may be biased, especially with respect to female crayfish. To determine if or when any migration occurs, future studies will need to search over a much larger area, or use tags of a type that facilitate reporting by the fishing public.

In summary, this study has provided new insights into the movement patterns of *Panulirus versicolor*. In particular, it is apparent that a large proportion of individuals have strong associations with small reef areas for considerable periods of time (at least at Northwest Island on the Great Barrier Reef). This information will be helpful when designing management strategies (*e.g*. marine protected areas) for this highly sought-after species.

CHAPTER 7: Social organisation and den utilisation

Abstract

Visual survey of 60 ha of coral reef at Northwest Island revealed 34 coral shelters (dens) that were occupied by painted crayfish (*Panulirus versicolor*), 85 of which were captured and tagged. Most dens contained only a single crayfish, but the distribution of crayfish was aggregated, since most crayfish were found in groups of 2−7 individuals. Daily visits to each den revealed that crayfish moved to and from nearby dens, such that the composition of groups changed frequently. Despite this, two male crayfish never occupied the same den simultaneously, indicating that groups were not merely random mixtures of individuals. Surprisingly, the relationship between body size (carapace length) and male social status (number of co-habiting females) was weak or non-existent, and experimental translocation of single crayfish to occupied dens did not result in eviction (at least not within 5−9 hr), regardless of body size or sex. Thus, the mechanisms driving this social system are subtle and require further investigation. With respect to the pattern of den utilisation, most crayfish in the population shared the 'best' 10−15 dens every day – a result that has important implications for the management of this popular fishery resource.

7.1 Introduction

Despite the importance of palinurid (spiny) lobsters to global fisheries and benthic ecology (Phillips 2006), relatively little is known about their behaviour. This is because individuals are nocturnal and not easily observed in the field (Atema and Cobb 1980). Furthermore, spiny lobsters are notoriously difficult to track in the wild, primarily due to problems associated with tag-loss during moulting. As a consequence, most studies of palinurid behaviour involve captive individuals (*e.g.* Zimmer-Faust and Spanier 1987; Glaholt 1990; Segura-Garcia *et al.* 2004). However, due to the inherent difficulty of simulating natural environments, it is not known to what degree behaviour in captivity is representative of that in the wild.

Most palinurids maintain a home range, throughout which they nocturnally forage for benthos (Chittleborough 1974; Jernakoff *et al.* 1987; MacDiarmid *et al.* 1991). During the day however, most species seek shelter in a den – an undercut or concave section of coral, rock or sponge (Atema and Cobb 1980; Herrnkind 1980). Because exposed individuals are more likely to be preyed upon than those under cover, it is thought that the principal function of the den is to provide protection from predators (Kanciruk 1980; Smith and Herrnkind 1992). The quality and availability of dens can therefore have a profound influence on the palinurid ecology (Eggleston and Lipcius 1992; Mintz *et al.* 1994; Herrnkind *et al.* 1997; Briones-Fourzan and Lozano-Alvarez 2001).

Although asocial during their larval and early benthic stages, adult palinurids can be found singly or in groups of up to 100 or more (Atema and Cobb 1980; Butler *et al.* 2006). Originally, den sharing was thought to have evolved as a result of the benefits afforded by group defence against predators (Atema and Cobb 1980). However, more recent studies suggest that den sharing may also be a consequence of conspecific attraction (the 'guide effect' hypothesis: Childress and Herrnkind 1997, 2001). In particular, it is thought that individuals are attracted to each other by a chemical odour (Zimmer-Faust *et al.* 1985;

Ratchford and Eggleston 2000) thereby reducing the time they are vulnerable to predators during the search for refuge (as occurs each morning after foraging away from the den).

Within the den, group-forming individuals frequently interact (*i.e.* engage in repeated contact). In captive situations, these interactions often result in the formation of size-based dominance hierarchies, whereby large individuals monopolise access to food, den space and potential mates (reviewed by Atema and Cobb 1980; Childress and Jury 2006). In some instances, subordinate individuals are forcibly evicted from their den (Kanciruk 1980; Segura-Garcia *et al*. 2004). Conspecific interactions would thus have the capacity to influence group composition. If this is the case, group structure may reflect the mating system of these animals.

It is thought that female palinurids mate no more than once per reproductive episode. Males, on the other hand, are capable of fertilising several females and they do not provide parental care (Aiken and Waddy 1980; Atema and Cobb 1980). If the sex-ratio of a population is close to uniformity, females are likely to be in short supply, since males can potentially fertilise more females than are available (Aiken and Waddy 1980; but see also MacDiarmid and Butler 1999). Under these circumstances, sociobiological theory predicts the formation of polygynous groups (harems) in which dominant (usually large) males defend females and (or) critical resources such as dens (Emlen and Oring 1977; Atema and Cobb 1980).

The objectives of this chapter were to (1) describe the social organisation and den utilisation of the painted crayfish (*Panulirus versicolor*) and (2) investigate the role of gender and body size in determining group composition. To achieve the first objective, groups of individuals occupying nearby dens were observed *in situ* on a daily basis (Experiment 1). To achieve the second objective, male and female crayfish of various sizes were introduced into dens containing established groups and observed for a short time thereafter (Experiment 2). In all cases, experimental animals were tagged with highly visible external tags (plastic zip-ties) to facilitate individual identification without the need for subsequent disturbance.

7.2 Materials and methods

7.2.1 Experiment 1 – social organisation and den utilisation

The study site, experimental animals and tagging techniques used in this chapter were the same as those described in Chapter 6. Briefly, 60 ha of coral reef at Northwest Island was censused during daylight for ten consecutive days on six occasions between December 2003 and December 2006. Each census involved a systematic search of all known dens in the area, and all newly-encountered crayfish were tagged and released.

The number and identity of crayfish inhabiting each den were recorded each day. An individual's residency time (RT) was calculated as the mean number of days of continuous residency at any one den. Den occupancy rate (DOR) was calculated as the mean number of crayfish per den per day. The greatest number of crayfish that were observed in a particular den at any one time was interpreted as the maximum den occupancy (MDO). With respect to RT and DOR, data were pooled across censuses due to small sample sizes.

At the completion of the study, the size of each den was recorded in terms of width, length and height, each measured using a standard rule. Internal volume was calculated as the product of these dimensions. Den construction (coral type) was also noted.

7.2.2 Data analyses

Multiple linear regression (Zar 1999) was used to assess the relationship between den size and MDO, and between den size and DOR. In both cases, den size was entered as width, length, height and volume, and variables were selected using the stepwise procedure described by Zar (1999). A one-way ANOVA was used to test for differences in mean DOR among dens of each coral type, and a *t* test was used to compare mean RT of males and females.

A χ^2 goodness-of-fit test was used to compare the distribution of group sizes to a random (Poisson) distribution (Zar 1999). Importantly, data were pooled into four categories (1, 2, 3 and ≥4 crayfish) so that expected frequencies were greater than two (Zar 1999). Vacant dens were excluded from the analysis (because they could not be identified) and Poisson probabilities were adjusted accordingly. To investigate the sex structure of crayfish groups, the distributions of males and females among different group sizes were compared to Poisson distributions using separate χ^2 goodness-of-fit tests. As before, data were pooled (three categories for males and four categories for females) so that expected frequencies were greater than two. The variance to mean ratio (VMR) was calculated in order to assess whether each distribution was aggregated (VMR > 1), random (VMR = 1) or uniform (VMR < 1) (Zar 1999).

To investigate the role of size in structuring social groups, male crayfish were categorised according to carapace length (CL; <125 mm = small; >125 mm = large) and social status (0 = solitary when first encountered; 1 = living with one female when first encountered; ≥2 = living with two or more females when first encountered). The effects of male size and social status on RT were then assessed by two-way, factorial ANOVA (Zar 1999). A one-way ANOVA was used to assess the relationship between body size (CL) and social status.

Although some of the same crayfish were repeatedly recaptured or resighted during successive censuses, only data from newly-encountered individuals were used for the calculation of RT, social status or group size, thus ensuring independence of observations. Occasionally, some individuals comprising a social group escaped before their identity could be ascertained. Accordingly, these 'incomplete' groups were excluded from the analyses.

7.2.3 Experiment 2 – manipulation of social groups

In December 2006 (*i.e.* immediately after the final census of Experiment 1), nine solitary crayfish ('intruders') were captured and translocated to nine different dens, each of which contained an established group consisting of 2–4 crayfish ('residents'). In each case, intruders were transported across distances of 38−262 m in a large water-filled tank onboard a support vessel (the combined handling and travel time for each translocation was approximately 5−15 min). Intruders were then released into the den, the occupants of which were identified retrospectively by their antennal tags (*n.b.* this enabled the sex and body size of all residents to be determined without disturbance). The behaviour of both residents and intruders was then observed *in situ* for approximately 20 min. All observations were made by the author from the den entrance with the aid of SCUBA, and care was taken to minimise disturbance to den occupants. Due to the logistical difficulties of catching and observing crayfish at night, all translocations were performed between 0800−1200 hr. Each den was then left undisturbed for a period of 5−9 hr, after which relevant dens were briefly revisited (during daylight) to check for changes in group composition. The same dens were also checked (during daylight) the next day.

Due to logistical difficulties, the maximum number of translocations that could be performed was nine. As such, the results of Experiment 2 are considered to be indicative of trends rather than conclusive.

7.3 Results

7.3.1 Experiment 1 – social organisation and den utilisation

Thirty-four useable dens (*i.e.* dens occupied by crayfish on at least one occasion) were identified at the study site. These dens ranged in volume from 0.03−0.65 m^3 and consisted of undercut sections of calcareous conglomerate (9%) or live coral (*Porites*, 70%;

Goniastrea, 15%; *Acropora*, 6%). Eighty-five adult *P. versicolor* were found to use these dens during the study period. No crayfish were observed outside a den.

Forty-seven crayfish (55%) were resighted 1−9 d after release, with each crayfish observed an average of 3.5 times. Ten crayfish were seen only at the den in which they were initially captured, although these crayfish were never seen again after 1−4 d. The remaining 37 individuals moved frequently within the study area, utilising up to four dens in any 10 d period. In most cases, these dens were in close proximity to each other (*i.e.* <400 m apart). Mean residency times (RT) of male and female crayfish were 2.3 ± 0.2 and 2.7 ± 0.3 d den^{-1}, respectively. These values were not significantly different (t test, $t_{84} = 1.06$, $p = 0.29$). Most tagged crayfish remained in the area for the duration of the study: 50 crayfish (59%) were resighted during more than one survey, while 30 crayfish (35%) were resighted during surveys that were at least 1 yr apart.

The number and identity of resident crayfish at each particular den were highly variable and often changed on a daily basis. In most cases, the number of crayfish found to use a particular den (at any time during the study) exceeded its maximum occupancy (MDO). Den volume was the only useful (significant) predictor of MDO (ANOVA, $F_{1,32} = 49.8$, $p < 0.001$, $r^2 = 0.60$), and it was typical for larger volume dens to accommodate larger groups (Figure 7.1a). Den volume was also the only useful (significant) predictor of den occupancy rate (DOR) (ANOVA, $F_{1,32} = 50.1$, $p < 0.001$, $r^2 = 0.61$), and it was typical for larger volume dens to be occupied more often than smaller volume dens (Figure 7.1b). Regardless of den size (volume), DOR was always well below MDO (*cf.* Figure 7.1a, b).

An average of 35% of dens were occupied each day and the relationship between DOR and coral type was not significant (ANOVA, $F_{3,30} = 0.58$, $p = 0.63$).

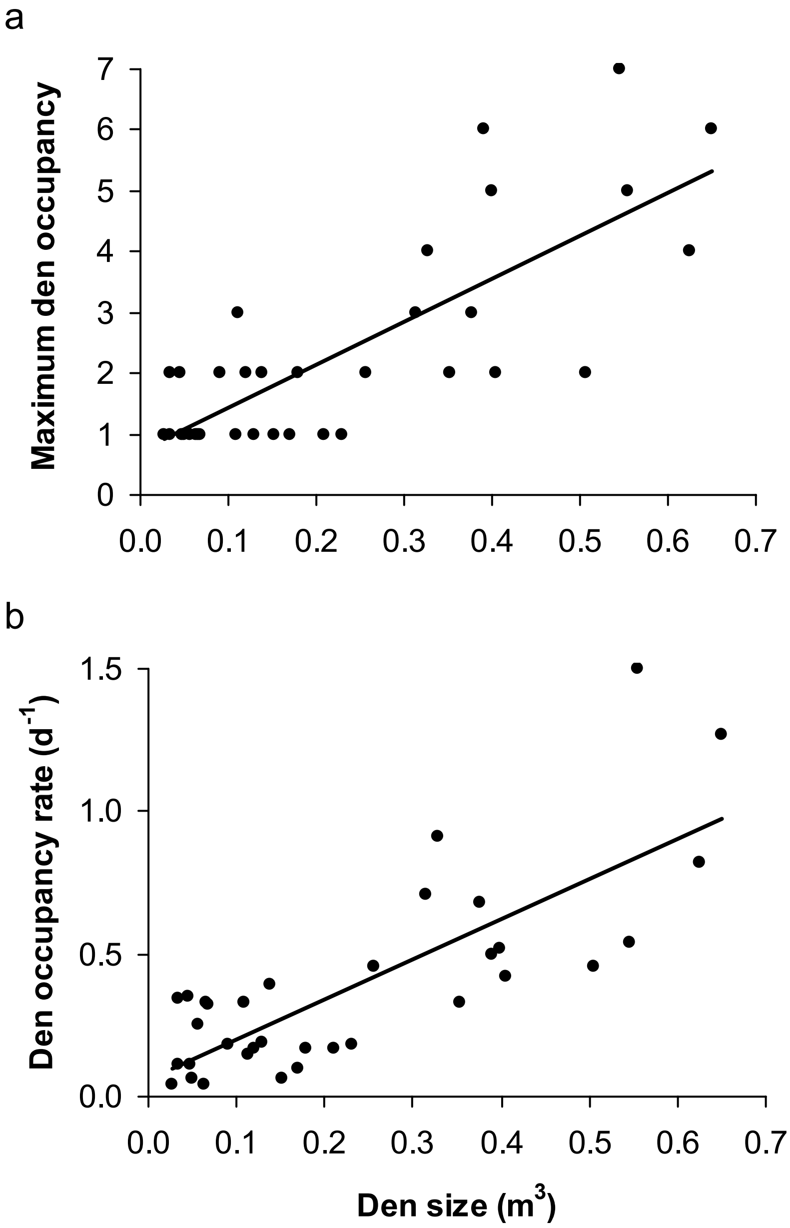

Figure 7.1 The relationship between den size and (a) maximum den occupancy (number of individuals) and (b) den occupancy rate for *Panulirus versicolor* at Northwest Island. See text for regression parameters.

When first encountered, 62% of dens contained only a single crayfish (Figure 7.2a), although 67% of crayfish were found in groups of 2−7 (Figure 7.2b). Crayfish were found in groups more often than expected by chance ($\chi^2_2 = 17.8$, $p < 0.001$, VMR = 1.34). Each group consisted of one male and one or more females. Females shared dens (with other females) more often than expected by chance ($\chi^2_2 = 8.2$, $p < 0.025$, VMR = 1.72), while males shared dens (with other males) less often than expected by chance ($\chi^2_1 = 16.0$, $p < 0.001$, VMR = 0.34). In fact, two or more adult males were never found together (Figure 7.2c).

The mean body size (CL) of male crayfish increased with increasing social status (Figure 7.3), although the relationship was not significant (ANOVA, $F_{2,30} = 1.19$, $p = 0.32$). Residency time was not significantly related to either social status (ANOVA, $F_{2,22} = 0.83$, $p = 0.45$) or body size ($F_{1,22} = 0.28$, $p = 0.61$), and interaction was not significant ($F_{2,22} = 0.33$, $p = 0.72$).

7.3.2 Experiment 2 – manipulation of social groups

Nine translocations were performed during the study; five involved a male intruder and four involved a female intruder. In terms of CL, two of the intruder males were smaller than the resident males, while three of the intruder males were larger than the resident males (*n.b.* each den contained only one resident male). The size of intruder females was generally within the size range of resident females, as most dens contained multiple females of different sizes (Table 7.1).

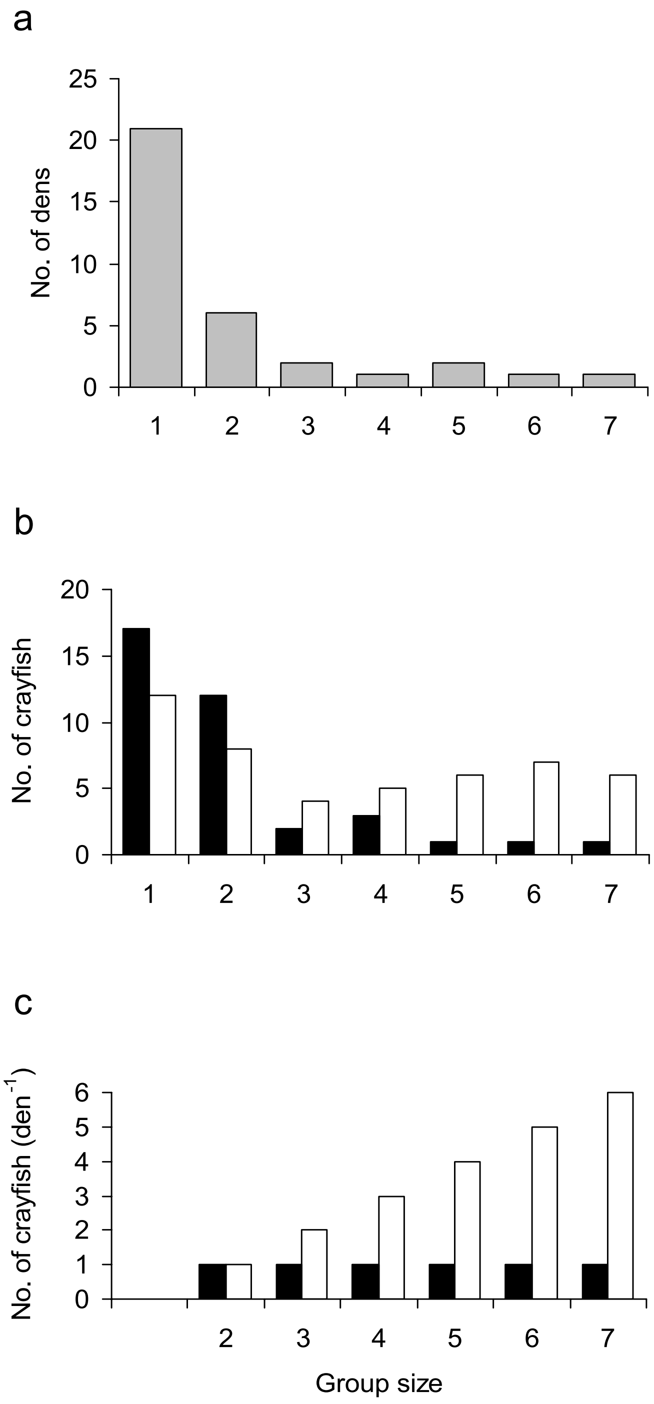

Figure 7.2 Patterns of den occupancy among social groups of *Panulirus versicolor* at Northwest Island: (a) the number of dens as a function of group size, (b) the total number of males (*black bars*) and females (*white bars*) as a function of group size, and (c) the sex-specific composition of social groups (males, *black bars*; females, *white bars*). Data were recorded during the first encounter with each den (a) or crayfish (b).

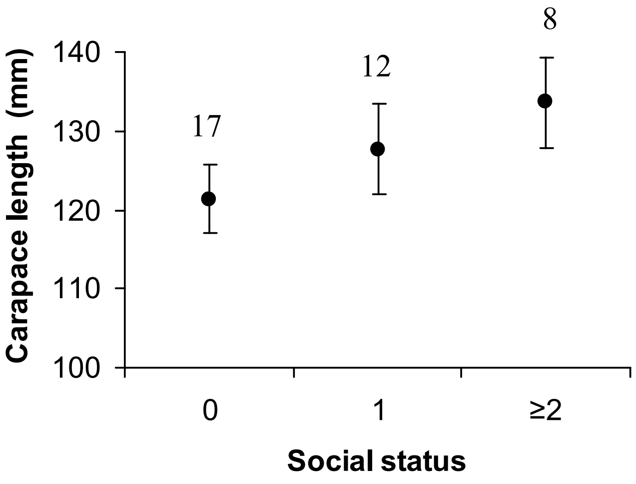

Figure 7.3 The relationship between mean carapace length (± SE) and social status in male *Panulirus versicolor* at Northwest Island. Social status refers to the number of females (0, 1 or ≥2) found with each male when it was first encountered. Differences between groups were not statistically significant ($p = 0.32$). Sample sizes are shown above each group.

All nine intruders moved rapidly into the den immediately after release. One female intruder retreated to an isolated part of a large den and appeared not to interact with any of the residents. The remaining eight intruders appeared to seek the company of one or more of the residents during a short search to find suitable refuge inside the den. Although both intruders and residents maintained defensive postures (*i.e.* crouched stance, abdomen tucked, tail fan folded, antennae pointed forward), there were no obvious signs of aggression by any individual. Instead, it was common for intruders to adopt a position next to (or on top of) one or more of the residents, such that body contact was extensive (*e.g.* mutual touching of antennae, pereiopods and carapace). When the intruder was male ($n = 5$), body contact with the resident male was observed on three occasions, while body contact with the resident female(s) was observed on four occasions. When the intruder was female ($n = 4$), body contact with the resident male was observed on two occasions, as was body contact with the resident female(s) (Table 7.1). In all cases, both intruders and residents remained in the den for at least 5−9 hr. However, many of the residents and all of the intruders had moved to other dens by the following day. None of the intruders was seen more than 9 hr after translocation (Table 7.1).

Table 7.1

The sex and body size (carapace length) of intruder and resident crayfish in relation to conspecific interactions and the duration of den occupation.

	Intruder		Residents			Observations		
Sample	Sex	Body size (mm CL)	Group size	Male body size (mm CL)	Female body size[a] (mm CL)	Aggression	Body contact[b]	Duration of den occupation[c] (hr)
1	Male	124	2	132	143	No	Male only	6−19
2	Male	149	3	137	125−129	No	Male & female	5−16
3	Male	135	2	127	129	No	Male & female	9−24
4	Male	137	4	130	95−142	No	Female only	6−23
5	Male	117	3	139	136−138	No	Female only	5−18
6	Female	122	3	140	105−132	No	Neither	7−19
7	Female	146	3	121	131−142	No	Male & female	5−16
8	Female	136	3	108	111−137	No	Male only	5−20
9	Female	121	3	136	115−137	No	Female only	8−22

[a] if two or more females were present, the size range is displayed

[b] refers to the sex of resident crayfish with which intruders were observed to make body contact (within 20 min of translocation)

[c] refers to the intruder

7.4 Discussion

This study investigated the social organisation and den utilisation of painted crayfish over periods of ten consecutive days. Unlike most other studies however, observations were made in the field. This is important given the degree to which captive conditions can influence the behaviour of wild animals (Cobb 1980).

Results indicate that tagged individuals maintained a home range within which they typically utilised several dens on consecutive days. Home ranges often overlapped, such that the same dens were regularly used by other individuals (either alone or together in a social group). Interestingly, the average time spent at each den was only 2−3 d (regardless of the size, sex or status of individual). This result reconciles a previous (anecdotal) observation that den residents are often ‘replaced’ shortly after their removal by local fishers (Author’s personal observation).

Although most dens contained single crayfish, most individuals were found in groups. In fact, groups of two or more were found more often than expected by chance. This suggests that individuals of *P. versicolor* are facultatively gregarious. Conspecific den-sharing has been identified among many other spiny lobsters (*e.g. Panulirus interruptus*, Zimmer-Faust and Spanier 1987; *Panulirus ornatus*, Trendall and Bell 1989; *Jasus edwardsii*, MacDiarmid 1994; *Panulirus argus*, Childress and Herrnkind 1997; *Panulirus guttatus*, Sharp *et al*. 1997), thus suggesting it is a ubiquitous feature of the Palinuridae.

Despite the gregarious nature of *P. versicolor*, two or more male crayfish never occupied the same den simultaneously. Rather, males were either solitary or associated with groups of 1−6 females. In contrast, most females were found in groups, and comparatively few were solitary. One hypothesis that might explain these observations is that females grouped themselves around preferred males (and excluded less-preferred males). This type of behaviour is expected under conditions of sperm limitation, because females would tend to seek larger (and presumably more fecund) males (MacDiarmid and Butler 1999). In *P. versicolor* however, the relationship between body size (CL) and social status (number of females) was weak or nonexistent − a result suggesting that social hierarchy is not solely determined by body size. An alternative hypothesis is that social organisation in *P. versicolor* is facultatively haremic, whereby males defend dens (or females) from other males. Interestingly, evidence of haremic social systems such as male den-guarding behaviour has been found among other palinurids (Kanciruk 1980; Lipcius *et al*. 1983; MacDiarmid *et al*. 1991; MacDiarmid 1994; Sharp *et al*. 1997). However, this type of behaviour was not apparent in *P. versicolor*: intruders appeared to seek the company of residents immediately after experimental translocation, and residents showed no signs of aggression toward intruders (regardless of size or sex). Perhaps resident males perceived the diver (observer) as a threat and survival actions overshadowed competitive behaviour. After all, palinurids are known to bunch together (*i.e.* engage in co-operative defence) when under threat from predators or divers (Kanciruk 1980; Herrnkind *et al*. 2001). Evidence refuting the 'den defence' hypothesis is thus circumstantial. It seems that remote videography (*e.g.* Jury *et al*. 2001) or perhaps even tethering experiments (*e.g.* Smith and Herrnkind 1992) will be required to resolve this enigma.

Given that dens provide protection from predators (Kanciruk 1980; Smith and Herrnkind 1992), one would expect that some dens are more 'attractive' than others. Indeed, larger volume dens generally sheltered more crayfish, more often. However, even the largest dens were occasionally vacant. This suggests that suitable dens are not limiting, and that den volume is not the only factor that influences which dens are occupied.

According to the 'guide effect' hypothesis, a den occupant represents a homing beacon guiding an exposed, vulnerable individual to a probable source of refuge (Childress and Herrnkind 1997). In this regard, crayfish are attracted to a den not because of its physical attributes, but because of other crayfish in it. One would predict, therefore, that palinurid group structure is flexible, since shelter-seeking individuals would be attracted to the nearest conspecific, regardless of their identity. In the case of *P. versicolor*, the composition of social groups changed regularly, and any association between two or more individuals was always short-lived (≤3 d). Despite this, social groups were not merely random mixtures of individuals, since each den contained only one male. Thus, patterns of den habitation in *P. versicolor* cannot be wholly explained by the 'guide effect' (unless of course its effects are sex-specific).

Patterns of den habitation by *P. versicolor* have significant implications with respect to fisheries management. Because individuals are sedentary during daylight, they are relatively easy to capture (using a speargun) once they have been found by a diver (Author's personal observation). Hence, on shallow coral reefs, *P. versicolor*'s principal refuge from fishing is the time required by divers to find occupied dens. At the study site (60 ha), the vast majority of tagged crayfish occupied the same 10−15 dens on any given day (these dens were typically the largest dens). From a fisher's perspective, this means that only 10−15 dens would need to be searched in order to find most of the crayfish in the area. Armed with this knowledge and a GPS unit, it would be possible for fishers to rapidly deplete the local crayfish population by finding, recording, and repeatedly visiting these dens. Thus, fishing regulations such as 'no take' areas may need to be expanded as GPS technology becomes increasingly available. This will be especially important on the Great Barrier Reef, since local crayfish populations are relatively small and thus easily over-fished (see Chapter 5).

It is possible that the results of this study were confounded by factors such as capture, handling, tagging and (or) repeated den visitation. However, this was considered to be unlikely because (1) crayfish were manually returned to their den after capture, (2) handling times were short (~5 min), (3) tags were small and unlikely to hinder the host (MacDiarmid *et al*. 1991; Frisch and Hobbs 2006), and (4) repeat visits to each den were unobtrusive and short in duration (<1 min). Furthermore, previous studies on the effects of capture and tagging on other palinurids found that these factors were unlikely to have lasting effects on the movement patterns and behaviour of experimental animals (Jernakoff *et al*. 1987; MacDiarmid *et al*. 1991). The data reported here are thus considered to be representative of crayfish that were not captured, handled, *et cetera*.

In summary, *P. versicolor* at Northwest Island had a gregarious distribution in which conspecifics frequently formed small groups in dens during the day. The composition of these groups was temporally variable with respect to individual membership, but rigid with respect to sex structure. Although the mechanisms driving this social system remain unresolved, it is clear that groups were not merely random mixtures of individuals. It is also clear that patterns of den habitation have significant consequences with respect to the catchability of *P. versicolor* and its vulnerability to over-exploitation. This information will be helpful when designing future management strategies for this important fishery resource.

CHAPTER 8: General Discussion

Painted crayfish are one of the most sought-after fishery resources on the Great Barrier Reef (GBR). However, due to the difficulties associated with studying this species (*e.g.* cryptic behaviour, low abundance, tag loss, avoidance of traps, dispersed landings of catches), little was known about either their biology or the characteristics of the fishery. Thus, the broad goal of this thesis was to describe the population biology and fishery ecology of painted crayfish on the GBR, *viz*. catch per unit effort (CPUE), total catch, size structure, abundance, reproduction, growth, mortality, movement patterns, sociology, and habitat utilisation. In general terms, this goal has been achieved (Chapters 2−7) and a basic scientific knowledge of painted crayfish now exists. The remaining sections of this thesis integrate the results from each chapter and explore potential management strategies that are aimed at ensuring the sustainability of this important fishery resource.

8.1 Potential management strategies

Painted crayfish are distributed throughout the GBR, from the Capricornia Cays in the south to the Torres Strait in the north (Kailola *et al*. 1993; Jones and Morgan 1994). Due to the long duration and extensive dispersal of palinurid larval stages (Phillips *et al*. 2006), painted crayfish on the GBR probably represent a single unit stock (see also Gargia-Rodriguez and Perez-Enriquez 2006; Matthee *et al*. 2007). Given that 20% of reefs in the region are protected from fishing (Fernandes *et al*. 2005), and many more are inaccessible to recreational fishers (Blamey and Hundloe 1993), conceivably there is a large unexploited breeding population. Thus, it is reasonable to assume that local overfishing would have little impact on the breeding potential of the unit stock (Pitcher 1993). The management significance of this is that there is little risk of recruitment overfishing of individual reefs (*e.g*. Northwest Island) because the source of recruitment is unlikely to be local. The main biological concern of management, then, should not be protection of breeding females, but optimisation of yield from the available stock (*e.g*. by implementing an appropriate minimum size limit; MSL). Currently, the situation in Queensland is the exact opposite: ovigerous and spermatophoric females are protected, but size limits are non-existent (Anon. 1995).

Yield of small-scale, palinurid fisheries is typically assessed *via* yield per recruit (YPR) analysis, since detailed catch and effort data are usually lacking (Pitcher 1993). The YPR model examines the trade-off between capturing a larger number of young (or small) individuals *versus* capturing a smaller number of old (or large) individuals, and is dependent upon growth, natural mortality, fishing mortality, and size at first capture (Beverton and Holt 1957). In practice, the latter two parameters are manipulated, at least hypothetically, to help identify management schemes that maximise yield. The model can be expressed as:

$$\mathrm{YPR} = W_\infty F e^{-M(t_\mathrm{c} - t_\mathrm{r})} \sum_{\mathrm{n}=0}^{3} [U_\mathrm{n} e^{-nK(t_\mathrm{c} - t_0)} / (F + M + nK)]$$

where $U_0 = 1$, $U_1 = -3$, $U_2 = 3$, $U_3 = -1$, W_∞ = mean asymptotic weight (from Figures 2.4 and 4.8), F = fishing mortality rate, M = natural mortality rate (from Table 5.2), K = growth co-efficient (from Figure 4.8), t_0 = hypothetical age at zero carapace length (from Figure 4.8), t_c = estimated age of crayfish when they reach the hypothetical MSL, and t_r = estimated age of crayfish when they first become vulnerable to the fishing gear. The latter parameter was assumed to be 1.8 yr, based on the lower size limit of painted crayfish that were captured by spearfishing at Palau (60 mm CL, MacDonald 1982) (*n.b.* size and age were inter-converted using the von Bertalanffy growth equation; see Chapter 4). Three hypothetical MSLs (80, 90 and 100 mm CL) were chosen for exploratory analysis, based on the dual criteria of size at first maturity (see Chapter 4) and ease of compliance by recreational fishers.

At a low fishing mortality (<0.3 yr^{-1}), implementation of a MSL is likely to have little effect on YPR in relation to the *status quo* (no MSL) (Figure 8.1a). At moderate to high fishing mortality (*e.g.* 0.5 yr^{-1}), however, implementation of a MSL is likely to increase YPR by 16−18% (Figure 8.1a) and increase population biomass by 44−90% (Figure 8.1b). The utility of a MSL will therefore depend on the level of fishing mortality, which is not presently known. Thus, future studies should seek to estimate this parameter by conducting field studies at locations known to be used by recreational fishers.

Surprisingly, YPR is relatively insensitive to variations in MSL between 80 and 100 mm CL, even at relatively high fishing mortality (Figure 8.1a). Hence, opting for a larger MSL, say 100 mm CL, is not likely to substantially reduce YPR, regardless of fishing mortality. Furthermore, if a MSL of 100 mm CL is implemented, a greater stock size would be maintained (Figure 8.1b) and every crayfish in the population would have the opportunity to breed at least once before capture (see section 4.4). Opting for a larger MSL would thus generate a greater safety margin against recruitment failure and reduce the effects of fishing selection on the gene pool.

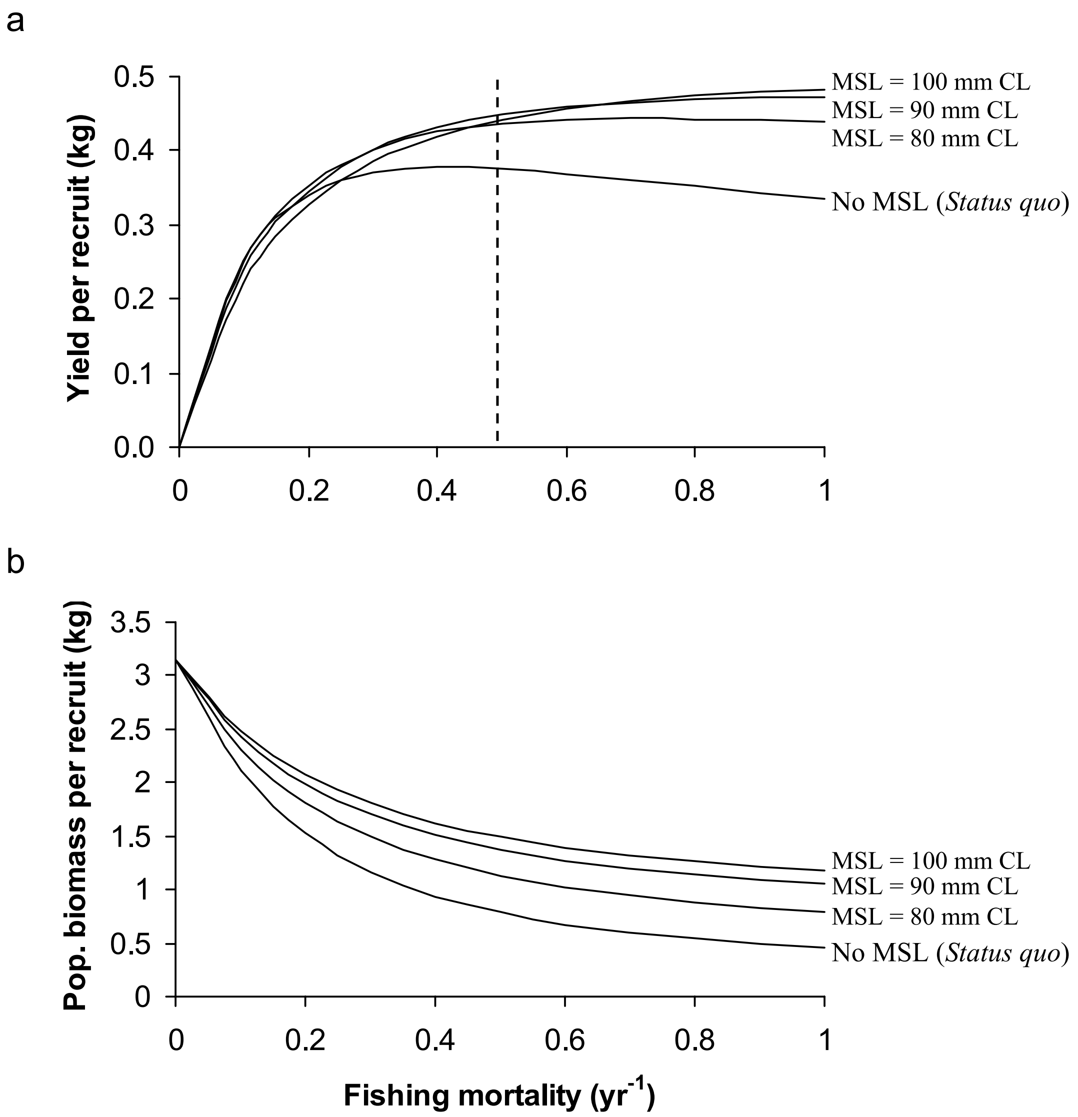

Figure 8.1 (a) Yield per recruit and (b) population biomass per recruit for a single cohort of *Panulirus versicolor* that are subject to various potential fishing mortality rates (F) and hypothetical minimum size limits (MSL). The vertical line shows $F_{0.1}$ for a MSL of 100 mm CL. Results are for individuals of ages 1−13 yr and a natural mortality rate (M) of 0.28 yr^{-1} (see Table 5.2). Mean age at recruitment to the fishery (t_r) is assumed to be 1.8 yr (carapace length ≈ 60 mm).

The YPR trajectory for a MSL of 100 mm CL is asymptotic (Figure 8.1a). Under such circumstances, optimum fishing mortality is typically assumed to be the value at which the slope of the YPR trajectory is one-tenth of its initial slope (*i.e.* $F_{0.1}$) (King 1995). For *P. versicolor*, $F_{0.1}$ is equivalent to 0.5 yr^{-1} (Figure 8.1a). Thus, it would be appropriate to cap fishing effort (*e.g.* by implementing catch limits) at a level that corresponds to a fishing mortality of 0.5 yr^{-1}, which is equivalent to removing approximately 39% of legal-sized crayfish annually. Given an estimated population size of 1400 (see Chapter 5), the maximum recommended harvest at Northwest Island is then 551 crayfish yr^{-1} (assumes MSL = 100 mm CL). However, without any MSL, the maximum recommended harvest is only 462 crayfish yr^{-1}.

8.2 Management recommendations

Although *P. versicolor* occurs in low abundance (Chapter 5), it is a highly sought-after seafood (Chapter 2). Individuals live in predictable places (Chapter 7) and maintain strong associations with small reef areas for long-term periods (Chapter 6). Together, these characteristics predispose *P. versicolor* to over-exploitation, which underscores the need to implement effective management strategies.

Based on the results of this study and assuming that a large proportion (*i.e.* 20−50%) of the GBR (and hence, a large proportion of the *P. versicolor* stock) remains inaccessible or protected by ‘no take’ reserves, three management strategies are recommended. Firstly, the current prohibition on possession of spermatophoric and ovigerous females should be revoked. This would eliminate the requirement to discard breeding females that are currently inadvertently killed by the fishery (*i.e.* reduce wastage; see Chapter 2).

The basis of this recommendation is that there appears to be little chance of localised recruitment overfishing and hence there is little need to protect breeding females at a local level (section 8.1). Secondly, introduction of a 100 mm CL MSL would optimise yield of the available stock (Figure 8.1a), maintain a greater population biomass regardless of fishing mortality (Figure 8.1b), and reduce the effects of fishing selection (section 8.1), all without greatly impacting current fishing practices (Figure 2.3). Thirdly, establishment of marine reserves is an effective management strategy to counteract localised depletion of adult *P. versicolor*, should this become a problem. These reserves need only be small (1−2 km in dimension), since adult individuals appear not to roam widely (Figure 6.1).

8.3 Concluding remarks

Much of the data used in this thesis were collected over a relatively small spatial scale, thus introducing the possibility that the estimated parameters may not be entirely representative of the GBR population as a whole. This is because biological characteristics of single species often vary among regions (MacDiarmid and Sainte-Marie 2006; Wahle and Fogarty 2006). Should this be the case and the current data were used to formulate management strategies for the entire GBR population (as in section 8.1), such strategies would be suboptimal. In fisheries elsewhere, this type of deficiency has provided the justification to preserve the *status quo* with respect to the proposed introduction or alteration of fisheries management regulations (Chubb 2000; Walters and Martell 2004). However, the current management scheme for *P. versicolor* is ‘data-less’ and is therefore based entirely on precautionary principles rather than on a sound knowledge of the species’ biology. Under these circumstances, ‘data-limited’ management is not just a valid alternative, but is a management imperative (Johannes 1998). This study provides a sound basis for the implementation of rational management strategies aimed at ensuring the sustainability of this highly desirable fishery resource.

Although the characteristics of palinurids in general have been reviewed many times (*e.g*. Kanciruk 1980; Lipcius and Eggleston 2000; Butler *et al*. 2006), there has not previously been any detailed study of the biology or ecology of *P. versicolor*. However, *P. versicolor* is potentially the most interesting palinurid because it is one of the more recently evolved species (George and Main 1967; George 1997; Patek *et al*. 2006). From the data gathered thus far, it seems that *P. versicolor* has retained a core set of ancestral traits that are ubiquitous across the Palinuridae, but has variously modified those traits to suit life in tropical, coral reef lagoons. For example, *P. versicolor* employs the same basic modes of growth and reproduction as do other palinurids but its moult intervals are shorter and its spawning periods are longer, presumably because it inhabits a-seasonal, tropical environments (Chapter 4). *Panulirus versicolor* also maintains a gregarious lifestyle, as do all of its congeners, but its principal place of refuge has (of necessity) shifted from rock ledges to live coral overhangs (Chapter 7). These results highlight the adaptability of the Palinuridae and the overall success of this group at exploiting a diversity of habitats.

The utility of this thesis extends well beyond its various biological discoveries. Firstly, the development and assessment of both elastomer implant and photographic identification techniques represent important technological advancements, since tracking palinurids through time and space has been a major obstacle for previous research on the biology and fishery ecology of this group. Secondly, results from Chapters Two (recreational harvest) and Five (demography) provide a valuable baseline for future stock assessments of *P. versicolor*. This is because CPUE can be used as an indicator of relative abundance, and size structure can be used as an indicator of relative fishing pressure (King 1995). As such, this thesis not only provides the basis for the implementation of sound, knowledge-based management strategies but also provides the framework upon which future studies can build. Given the importance of *P. versicolor* to the GBR recreational fishery and the current lack of knowledge about them, the scope for future research on these animals remains broad and the need for that research remains urgent.

REFERENCES

Acosta CA (1999) Benthic dispersal of Caribbean spiny lobsters among insular habitats: implications for the conservation of exploited marine species. *Conservation Biology* 13: 603-612

Aiken DE (1980) Moulting and growth. In: Cobb JS, Phillips BF (eds) *The Biology and Management of Lobsters* (vol. 1). Academic Press, New York, pp 91-163

Aiken DE, Waddy SL (1980) Reproductive biology. In: Cobb JS, Phillips BF (eds) *The Biology and Management of Lobsters* (vol. 1). Academic Press, New York, pp 215-276

Alcock J (1998) *Animal Behavior: An Evolutionary Approach*. Sinauer Associates, Massachusetts

Anderson SD, Goldman KJ (1996) Photographic evidence of white shark movements in California waters. *California Fish and Game* 82: 182-186

Andrew NL, MacDiarmid AB (1991) Interrelations between sea urchins and spiny lobsters in northeastern New Zealand. *Marine Ecology Progress Series* 70: 211-222

Annala JH, Bycroft BL (1988) Growth of rock lobsters (*Jasus edwardsii*) in Fiordland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 22: 29-41

Annala JH, Sullivan KJ (1997) Management strategies in lobster fisheries: report from a workshop. *Marine and Freshwater Research* 48: 1081-1083

Anonymous (1990) *Reader's Digest Book of the Great Barrier Reef*. Reader's Digest, Sydney

Anonymous (1995) *Fisheries Regulation*. Queensland Government, Brisbane (accessed *via* www.legislation.qld.gov.au on 1-9-2007)

Arzoumanian Z, Holmberg J, Norman B (2005) An astronomical pattern matching algorithm for computer aided identification of whale sharks, *Rhincodon typus*. *Journal of Applied Ecology* 42: 999-1011

Atema J, Cobb JS (1980) Social behavior. In: Cobb JS, Phillips BF (eds) *The Biology and Management of Lobsters* (vol. 1). Academic Press, New York, pp 409-450

Balazs GH (1973) A simplified method for identifying experimental shrimp. *Progressive Fish-Culturist* 35: 27

Bannister RCA, Addison JT, Lovewell SRJ (1994) Growth, movement, recapture rate and survival of hatchery-reared lobsters (*Homarus gammarus*) released into the wild on the English east coast. *Crustaceana* 67: 156-172

Belk MC, Houston DD (2002) Bergmann's rule in ectotherms: a test using freshwater fishes. *American Naturalist* 160: 803-808

Bell RS, Channells PW, MacFarlane JW, Moore R, Phillips BF (1987) Movements and breeding of the ornate rock lobster, *Panulirus ornatus*, in Torres Strait and on the north-east coast of Queensland. *Australian Journal of Marine and Freshwater Research* 38: 197-210

Bergman PK, Haw F, Blankenship HL, Buckley RM (1992) Perspectives on design, use, and misuse of fish tags. *Fisheries* 17: 20-25

Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. *Fisheries Investigations* (London) Series 2: 19

Blamey RK, Hundloe TJ (1993) *Characteristics of Recreational Boat Fishing in the Great Barrier Reef Region*. Great Barrier Reef Marine Park Authority, Townsville

Booth JD (2000) New Zealand's rock lobster fisheries. In: Phillips BF, Kittaka J (eds) *Spiny Lobsters: Fisheries and Culture*. Blackwell Science Publishers, Oxford, pp 78-89

Briones-Fourzan P, Lozano-Alvarez E (2001) Effects of artificial shelters (casitas) on the abundance and biomass of juvenile spiny lobsters *Panulirus argus* in a habitat-limited tropical reef lagoon. *Marine Ecology Progress Series* 221: 221-232

Butler MJ, Herrnkind WF (2000) Puerulus and juvenile ecology. In: Phillips BF, Kittaka J (eds) *Spiny Lobsters: Fisheries and Culture*. Blackwell Science Publishers, Oxford, pp 276-301

Butler MJ, Steneck RS, Herrnkind WF (2006) Juvenile and adult ecology. In: Phillips BF (ed) *Lobsters: Biology, Management, Aquaculture and Fisheries*. Blackwell Publishing, Oxford, pp 263-309

Cadwallader P, Russell M, Cameron D, Bishop M, Tanzer J (2000) Achieving ecologically sustainable fisheries in the Great Barrier Reef World Heritage Area *Proceedings of the Ninth International Coral Reef Symposium*, Bali, Indonesia, pp 697-704

Caputi N, Chubb C, Melville-Smith R, Pearce A, Griffin D (2003) Review of relationships between life history stages of the western rock lobster, *Panulirus cygnus*, in Western Australia. *Fisheries Research* 65: 47-61

Childress M, Herrnkind WF (1997) Den sharing by juvenile Caribbean spiny lobsters (*Panulirus argus*) in nursery habitat: cooperation or coincidence? *Marine and Freshwater Research* 48: 751-758

Childress MJ, Herrnkind WF (2001) The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. *Animal Behavior* 62: 465-472

Childress MJ, Jury SH (2006) Behaviour. In: Phillips BF (ed) *Lobsters: Biology, Management, Aquaculture and Fisheries*. Blackwell Publishing, Oxford, pp 78-112

Chittleborough RG (1974) Home range, homing and dominance in juvenile western rock lobsters. *Australian Journal of Marine and Freshwater Research* 25: 227-234

Chubb CF (2000) Reproductive biology: issues for management. In: Phillips BF, Kittaka J (eds) *Spiny Lobsters: Fisheries and Culture*. Blackwell Science Publishers, Oxford, pp 245-275

Cobb JS (1980). Introduction. In: Cobb JS, Phillips BF (eds) *The Biology and Management of Lobsters* (vol. 1). Academic Press, New York, pp 345-347

Cobb JS, Phillips BF (1980) *The Biology and Management of Lobsters*. Academic Press, New York

Connolly NA, Brown TL (1995) Use of angler diaries to examine biases associated with 12-months recall on mail questionnaires. *Transactions of the American Fisheries Society* 124: 413-442

Cooke SJ, Cowx IG (2004) The role of recreational fishing in global fish crises. *Bioscience* 54: 857-859

Courtney AJ, Cosgrove MG, Die DJ (2001) Population dynamics of scyllarid lobsters of the genus *Thenus* spp. on the Queensland (Australia) east coast I. Assessing the effects of tagging. *Fisheries Research* 53: 251-261

Dalzell P, Adams TJH, Polunin NVC (1996) Coastal fisheries in the Pacific Islands. *Oceanography and Marine Biology: An Annual Review* 34: 395-531

Davis GE (1981) Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management. *Fishery Bulletin* 78: 979-984

Dennis DM, Pitcher CR, Skewes TD (2001) Distribution and transport pathways of *Panulirus ornatus* (Fabricius, 1776) and *Panulirus* spp. larvae in the Coral Sea, Australia. *Marine and Freshwater Research* 52: 1175-1185

Dennis DM, Skewes TD, Pitcher CR (1997) Habitat use and growth of juvenile ornate rock lobsters, *Panulirus ornatus* (Fabricius, 1798), in Torres Strait, Australia. *Marine and Freshwater Research* 48: 663-670

Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1: 95-107

Dubula O, Groeneveld JC, Santos J, van Zyl DL, Brouwer SL, van den Heever N, McCue SA (2005) Effects of tag-related injuries and timing of tagging on growth of rock lobster, *Jasus lalandii*. *Fisheries Research* 74: 1-10

Dunham DW (1978) Effect of chela white on agonistic success in a diogenid hermit crab (*Calcinus laevimanus*). *Marine Behaviour and Physiology* 5: 137-144

Ebert TA, Ford RF (1986) Population ecology and fishery potential of the spiny lobster *Panulirus penicillatus* at Enewetak Atoll, Marshall Islands. *Bulletin of Marine Science* 38: 56-67

Eggleston DB, Lipcius RN (1992) Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. *Ecology* 73: 992-1011

Emlen ST, Oring W (1977) Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215-223

Ennis GP (1986) Sphyrion tag loss from the American lobster, *Homarus americanus*. *Transactions of the American Fisheries Society* 115: 914-917

Fernandes L, Day J, Lewis A, Slegers S, Kerrigan B, Breen D, Cameron D, Jago B, Hall J, Lowe D, Innes J, Tanzer J, Chadwick V, Thompson L, Gorman K, Simmons M, Barnett B, Sampson K, De'Ath G, Mapstone B, Marsh H, Possingham H, Ball I, Ward T, Dobbs K, Aumend J, Slater D, Stapleton K (2005) Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on marine protected areas. *Conservation Biology* 19: 1733-1744

Forcucci D, Butler MJ, Hunt JH (1994) Population dynamics of juvenile Caribbean spiny lobster, *Panulirus argus*, in Florida Bay, Florida. *Bulletin of Marine Science* 54: 805-818

Frisch AJ (2005) Bachelors seek house and harem: a new tagging technique reveals the cryptic world of crayfish on coral reefs. *Australasian Science* 26: 41-42

Frisch AJ (2007a) Growth and reproduction of the painted spiny lobster (*Panulirus versicolor*) on the Great Barrier Reef (Australia). *Fisheries Research* 85: 61-67

Frisch AJ (2007b) Short- and long-term movements of painted lobster (*Panulirus versicolor*) on a coral reef at Northwest Island, Australia. *Coral Reefs* 26: 311-317

Frisch AJ (2008) Social organisation and den utilisation of painted spiny lobster (*Panulirus versicolor*) on a coral reef at Northwest Island, Australia. *Marine and Freshwater Research* (In press; accepted 24-9-2007)

Frisch AJ, Hobbs J-PA (2006) Long-term retention of internal elastomer tags in a wild population of painted crayfish (*Panulirus versicolor* [Latreille]) on the Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 339: 104-110

Frisch AJ, Hobbs J-PA (2007) Photographic identification based on unique, polymorphic colour patterns: a novel method for tracking a marine crustacean. *Journal of Experimental Marine Biology and Ecology* 351: 294-299

Frisch AJ, Baker R, Hobbs J-PA, Nankervis L (2008) A quantitative comparison of recreational spearfishing and linefishing on the Great Barrier Reef: implications for management of multi-sector coral reef fisheries. *Coral Reefs* 27: 85-95

Gargia-Rodriguez FJ, Perez-Enriquez R (2006) Genetic differentiation of the California spiny lobster *Panulirus interruptus* (Randall, 1840) along the west coast of the Baja California Peninsula, Mexico. *Marine Biology* 148: 621-629

George RW (1968) Tropical spiny lobsters, *Panulirus* spp., of Western Australia (and the Indo-West Pacific). *Journal of the Royal Society of Western Australia* 51: 33-38

George RW (1974) Coral reefs and rock lobster ecology in the Indo-West Pacific region *Proceedings of the Second International Coral Reef Symposium*, Brisbane, Australia, pp 321-325

George RW (1997) Tectonic plate movements and the evolution of *Jasus* and *Panulirus* spiny lobsters (Palinuridae). *Marine and Freshwater Research* 48: 1121-1130

George RW, Main AR (1967) The evolution of spiny lobsters (Palinuridae): a study of evolution in the marine environment. *Evolution* 21: 803-820

George RW, Morgan GJ (1979) Linear growth stages in the rock lobster (*Panulirus versicolor*) as a method for determining size at first physical maturity. *Rapports et Proces-verbaux des Reunion, Conseil International pour l'Exploration de la Mer* 175: 182-185

Ghidalia W (1985) Structural and biological aspects of pigments. In: Bliss DE, Mantel LH (eds) *The Biology of Crustacea: Integument, Pigments and Hormonal Processes*. Academic Press, London, pp 301-394

Glaholt RD (1990) Social behavior and habitat use of captive juvenile spiny lobster, *Panulirus argus* (Latreille, 1804) (Decapoda, Palinuridae). *Crustaceana* 58: 200-206

Godin DM, Carr WH, Hagino G, Segura F, Sweeney JN, Blankenship L (1996) Evaluation of a fluorescent elastomer internal tag in juvenile and adult shrimp, *Penaeus vannamei*. *Aquaculture* 139: 243-248

Gonzalez-Yanez AA, Millan RP, De Leon ME, Cruz-Font L, Wolff M (2006) Modified Delury depletion model applied to spiny lobster, *Panulirus argus* (Latreille, 1804) stock, in the southwest of the Cuba shelf. *Fisheries Research* 79: 155-161

Groeneveld JC (1997) Growth of spiny lobster *Palinurus gilchristi* (Decapoda: Palinuridae) off South Africa. *South African Journal of Marine Science* 18: 19-29

Gulland JA, Holt SJ (1959) Estimation of growth parameters for data at unequal time intervals. *Journal du Conseil International pour l'Exploration de la Mer* 25: 47-49

Hall-Spencer JM, Moore PG, Sneddon LU (1999) Observations and possible function of the striking anterior coloration pattern of *Galathea intermedia* (Crustacea: Decapoda: Anomura). *Journal of the Marine Biological Association of the United Kingdom* 79: 371-372

Hammond PS, Mizroch SA, Donovan GP (1990) *Individual Recognition of Cetaceans: Use of Photo-identification and Other Techniques to Estimate Population Parameters*. International Whaling Commission, Cambridge

Heibo E, Magnhagen C, Vollestad LA (2005) Latitudinal variation in life-history traits in Eurasian perch. *Ecology* 86: 3377-3386

Henry GW, Lyle JM (2003) *The National Recreational and Indigenous Fishing Survey*. Australian Government Department of Agriculture, Fisheries and Forestry, Canberra

Herrnkind WF (1980) Spiny lobsters: patterns of movement. In: Cobb JS, Phillips BF (eds) *The Biology and Management of Lobsters* (vol. 1). Academic Press, New York, pp 349-407

Herrnkind WF, Butler MJ, Hunt JH, Childress M (1997) Role of physical refugia: implications from a mass sponge die-off in a lobster nursery in Florida. *Marine and Freshwater Research* 48: 759-769

Herrnkind WF, Childress MJ, Lavalli KL (2001) Cooperative defence and other benefits among exposed spiny lobsters: inferences from group size and behaviour. *Marine and Freshwater Research* 52: 1113-1124

Holthius LB (1991) *Marine Lobsters of the World*. FAO species catalogue (Vol. 13, No. 125). Food and Agriculture Organisation of the United Nations, Rome

Hundloe T (1985) *Fisheries of the Great Barrier Reef*. Prestige Litho Printing, Brisbane

Hunt JH (2000) Status of the fishery for *Panulirus argus* in Florida. In: Phillips BF, Kittaka J (eds) *Spiny Lobsters: Fisheries and Culture*. Blackwell Science Publishers, Oxford, pp 189-199

Jennings S, Kaiser MJ, Reynolds JD (2001) *Marine fisheries ecology*. Blackwell Science, Oxford

Jernakoff P, Phillips BF, Maller RA (1987) A quantitative study of nocturnal foraging distances of the western rock lobster *Panulirus cygnus* George. *Journal of Experimental Marine Biology And Ecology* 113: 9-21

Jerry DR, Stewart T, Purvis IW, Piper LR (2001) Evaluation of visual implant elastomer and alphanumeric internal tags as a method to identify juveniles of the freshwater crayfish, *Cherax destructor*. *Aquaculture* 193: 149-154

Johannes RE (1998) The case for data-less marine resource management: examples from tropical nearshore fisheries. *Trends in Ecology and Evolution* 13: 243-246

Jones DS, Morgan GJ (1994) *A Field Guide to Crustaceans of Australian Waters*. Reed, Chatswood, NSW

Jury SH, Howell H, O'Grady DF, Watson WH, 2001. Lobster trap video: *in situ* surveillance of the behaviour of *Homarus americanus* in and around traps. *Marine and Freshwater Research* 52: 1125-1132

Kailola PJ, Williams MJ, Stewart PC, Reichelt RE, McNee A, Grieve C (1993) *Australian fisheries resources*. Bureau of Resource Sciences, Canberra

Kanciruk P (1980) Ecology of juvenile and adult Palinuridae (spiny lobsters). In: Cobb JS, Phillips BF (eds) *The Biology and Management of Lobsters* (vol. 2). Academic Press, New York, pp 59-96

Kelly S, MacDiarmid AB (2003) Movement patterns of mature spiny lobsters, *Jasus edwardsii*, from a marine reserve. *New Zealand Journal of Marine and Freshwater Research* 37: 149-158

King M (1995) *Fisheries Biology, Assessment and Management*. Fishing News Books, Oxford

Krebs C, J. (1999) *Ecological Methodology*. Addison-Welsey Educational Publishers, Menlo Park, U.S.A.

Kulbicki M, Guillemot N, Amand M (2005) A general approach to length-weight relationships for New Caledonian lagoon fishes. *Cybium* 29: 235-252

Kuthalingam MDK, Luther G, Lazarus S (1980) Rearing of early juveniles of spiny lobster *Panulirus versicolor* (Latreille) with notes on lobster fishery in Vizhinjam area. *Indian Journal of Fisheries* 27: 17-23

Lincoln-Smith MP, Bell JD, Pollard DA, Russell BC (1989) Catch and effort of competition spearfishermen in Southeastern Australia. *Fisheries Research* 8: 45-61

Linnane A, Mercer JP (1998) A comparison of methods for tagging juvenile lobsters (*Homarus gammarus* L.) reared for stock enhancement. *Aquaculture* 163: 195-202

Lipcius RN, Edwards ML, Herrnkind WF, Waterman SA (1983) *In situ* mating behavior of the spiny lobster *Panulirus argus*. *Journal of Crustacean Biology* 3: 217-222

Lipcius RN, Eggleston DB (2000) Ecology and fishery biology of spiny lobsters. In: Phillips BF, Kittaka J (eds) *Spiny Lobsters: Fisheries and Culture*. Blackwell Science, Oxford, pp 1-41

Lozano-Alvarez E, Briones-Fourzan P, Phillips BF (1991) Fishery characteristics, growth, and movements of the spiny lobster *Panulirus argus* in Bahia de la Ascension, Mexico. *Fishery Bulletin* 89: 79-89

Lozano-Alvarez E, Briones-Fourzan P, Ramos-Aguilar ME (2003) Distribution, shelter fidelity, and movements of subadult spiny lobsters (*Panulirus argus*) in areas with artificial shelters (casitas). *Journal of Shellfish Research* 22: 533-540

MacDiarmid AB (1991) Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster *Jasus Edwardsii* on a coastal reef in northern New Zealand. *Marine Ecology Progress Series* 70: 129-141

MacDiarmid AB (1994) Cohabitation in the spiny lobster *Jasus edwardsii* (Hutton, 1875). *Crustaceana* 66: 341-355

MacDiarmid AB, Butler MJ (1999) Sperm economy and limitation in spiny lobsters. *Behavioural Ecology and Sociobiology* 46: 14-24

MacDiarmid AB, Sainte-Marie B (2006) Reproduction. In: Phillips BF (ed) *Lobsters: Biology, Management, Aquaculture and Fisheries*. Blackwell Publishing, Oxford, pp 45-77

MacDiarmid AB, Hickey B, Maller RA (1991) Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. *Journal of Experimental Marine Biology and Ecology* 147: 185-205

MacDonald CD (1982) Catch composition and reproduction of the spiny lobster *Panulirus versicolor* at Palau. *Transactions of the American Fisheries Society* 111: 694-699

MacFarlane JW, Moore R (1986) Reproduction of the ornate rock lobster, *Panulirus ornatus* (Fabricius), in Papua New Guinea. *Australian Journal of Marine and Freshwater Research* 37: 55-65

Mann BQ, Scott GM, Mann-Lang JB, Brouwer SL, Lamberth SJ, Sauer WHH, Erasmus C (1997) An evaluation of participation in and management of the South African spearfishery. *South African Journal of Marine Science* 18: 179-193

Matthee CA, Cockcroft AC, Gopal K, von der Heyden S (2007) Mitochondrial DNA variation of the west-coast rock lobster, *Jasus lalandii*: marked genetic diversity differences among sampling sites. *Marine and Freshwater Research* 58: 1130-1135

Mauchline J (1977) Growth of shrimps, crabs and lobsters - an assessment. *Journal du Conseil International pour l'Exploration de la Mer* 37: 162-169

McGarvey R, Ferguson GJ, Prescott JH (1999) Spatial variation in mean growth rates at size of southern rock lobster, *Jasus edwardsii*, in South Australian waters. *Marine and Freshwater Research* 50: 333-342

McPherson R (2002) Assessment of T-bar anchor tags for marking the blue swimmer crab *Portunus pelagicus* (L.). *Fisheries Research* 54: 209-216

Melville-Smith R, Chubb CF (1997) Comparison of dorsal and ventral tag retention in western rock lobsters, *Panulirus cygnus* (George). *Marine and Freshwater Research* 48: 577-580

Mintz JD, Lipcius RN, Eggleston DB, Seebo MS (1994) Survival of juvenile Caribbean spiny lobster: effects of shelter size, geographic location and conspecific abundance. *Marine Ecology Progress Series* 112: 255-266

Moore R, MacFarlane JW (1984) Migrations of the ornate rock lobster, *Panulirus ornatus* (Fabricius), in Papua New Guinea. *Australian Journal of Marine and Freshwater Research* 35: 197-212

Morgan GR (1974) Aspects of the population dynamics of the western rock lobster, *Panulirus cygnus* George. I. Estimation of population density. *Australian Journal of Marine and Freshwater Research* 25: 235-248

Morgan GJ (1980) Population dynamics of spiny lobsters. In: Cobb JS, Phillips BF (eds) *The Biology and Management of Lobsters* (vol. 2). Academic Press, New York, pp 189-217

Muller RG, Hunt JH, Matthews TR, Sharp WC (1997) Evaluation of effort reduction in the Florida Keys spiny lobster, *Panulirus argus*, fishery using an age-structured population analysis. *Marine and Freshwater Research* 48: 1045-1058

Munro JL (2000) Fisheries for spiny lobsters in the tropical Indo-west Pacific. In: Phillips BF, Kittaka J (eds) *Spiny Lobsters: Fisheries and Culture*. Blackwell Science, Oxford, pp 90-97

Newman SJ, Williams AM, Russ GR (1997) Patterns of zonation of assemblages of the Lutjanidae, Lethrinidae and Serranidae (Epinephelinae) within and among mid-shelf and outer-shelf reefs in the central Great Barrier Reef. *Marine and Freshwater Research* 48: 119-128

Parsons DM, Eggleston DB (2005) Indirect effects of recreational fishing on behavior of the spiny lobster *Panulirus argus*. *Marine Ecology Progress Series* 303: 235-244

Parsons DM, Eggleston DB (2007) Potential population and economic consequences of sublethal injuries in the spiny lobster fishery of the Florida Keys. *Marine and Freshwater Research* 58: 166-177

Patek SN, Feldmann RM, Porter M, Tshudy M (2006) Phylogeny and evolution. In: Phillips BF (ed) *Lobsters: Biology, Management, Aquaculture and Fisheries*. Blackwell Publishing, Oxford, pp 113-145

Pauly D (1983) Length-converted catch curves: a powerful tool for fisheries research in the tropics. *ICLARM Fishbyte* 1: 9-13

Pennycuick CJ (1978) Identification using natural markings. In: Stonehouse B (ed) *Animal Marking*. Macmillan Press, London, pp 147-159

Persat H (1982) Photographic identification of individual grayling (*Thymallus thymallus*) based on the disposition of black dots and scales. *Freshwater Biology* 12: 97-101

Phillips BF (1983) Migrations of pre-adult western rock lobsters, *Panulirus cygnus*, in Western Australia. *Marine Biology* 76: 311-318

Phillips BF (2006) *Lobsters: Biology, Management, Aquaculture and Fisheries*. Blackwell Publishing, Oxford

Phillips BF, Kittaka J (2000) *Spiny Lobsters: Fisheries and Culture*. Blackwell Science, Oxford

Phillips BF, Melville-Smith R (2006) *Panulirus* species. In: Phillips BF (ed) *Lobsters: Biology, Management, Aquaculture and Fisheries*. Blackwell Publishing, Oxford, pp 359-384

Phillips BF, Sastry AN (1980) Larval ecology. In: Cobb JS, Phillips BF (eds) *The Biology and Management of Lobsters* (vol. 2). Academic Press, New York, pp 11-57

Phillips BF, Booth JD, Cobb JS, Jeffs AG, McWilliam P (2006) Larval and postlarval ecology. In: Phillips BF (ed) *Lobsters: Biology, Management, Aquaculture and Fisheries*. Blackwell Publishing, Oxford, pp 231-262

Phillips BF, Chubb CF, Melville-Smith R (2000) The status of Australia's rock lobster fisheries. In: Phillips BF, Kittaka J (eds) *Spiny Lobsters: Fisheries and Culture*. Blackwell Science, Oxford, pp 45-77

Phillips BF, Cobb JS, George RW (1980) General Biology. In: Cobb JS, Phillips BF (eds) *The Biology and Management of Lobsters* (vol 1). Academic Press, New York, pp 1-82

Phillips BF, Joll LM, Sandland RL, Wright D (1983) Longevity, reproductive condition, and growth of the western rock lobster, *Panulirus cygnus* George, reared in aquaria. *Australian Journal of Marine and Freshwater Research* 34: 419-429

Phillips BF, Palmer MJ, Cruz R, Trendall J (1992) Estimating growth of the spiny lobsters *Panulirus cygnus*, *P. argus* and *P. ornatus*. *Australian Journal of Marine and Freshwater Research* 43: 1177-1188

Pillai CSG, Mohan M, Kunhikoya KK (1985) Observations on the lobsters of Minicoy Atoll. *Indian Journal of Fisheries* 32: 112-122

Pitcher CR (1993) Spiny lobster. In: Wright A, Hill L (eds) *Nearshore Marine Resources of the South Pacific*. Forum Fisheries Agency, Honiara, pp 539-607

Pitcher CR, Dennis DM, Skewes TD (1997) Fishery-independent surveys and stock assessment of *Panulirus ornatus* in Torres Strait. *Marine and Freshwater Research* 48: 1059-1067

Pitcher CR, Skewes TD, Dennis DM, Prescott JH (1992) Estimation of the abundance of the tropical lobster *Panulirus ornatus* in Torres Strait, using visual transect-survey methods. *Marine Biology* 113: 57-64

Randall DJ, Burggren W, French K (2002) *Animal Physiology: Mechanisms and Adaptations*. W.H. Freeman and Company, New York

Randall JE, Allen GR, Steene RC (1990) *Fishes of the Great Barrier Reef and Coral Sea*. Crawford House Press, Bathurst, Australia

Ratchford SG, Eggleston DB (2000) Temporal shift in the presence of a chemical cue contributes to a diel shift in sociality. *Animal Behavior* 59: 793-799

Roberts CM, Polunin NVC (1991) Are marine reserves effective in the management of fisheries? *Reviews in Fish Biology and Fisheries* 1: 65-91

Robertson DN, Butler MJ (2003) Growth and size at maturity in the spotted spiny lobster, *Panulirus guttatus*. *Journal of Crustacean Biology* 23: 265-272

Rowe S, Haedrich RL (2001) Streamer tag-loss from American lobsters. *Transactions of the American Fisheries Society* 130: 516-518

Ruddle K (1996) Geography and human ecology of reef fisheries. In: Polunin NVC, Roberts CM (eds) *Reef Fisheries*. Chapman and Hall, London, pp 137-160

Scarrat DJ (1970) Laboratory and field tests of modified sphyrion tags on lobsters (*Homarus americanus*). *Journal of the Fisheries Research Board of Canada* 27: 257-264

Seber GAF (1973) *The Estimation of Animal Abundance and Related Parameters*. Griffin, London

Segura-Garcia I, Lozano-Alvarez E, Briones-Fourzan P (2004) Within-shelter behaviour of the spotted spiny lobster, *Panulirus guttatus* (Latreille), in simulated communal dens: an exploratory study. *Marine and Freshwater Behavior and Physiology* 37: 17-30

Sharp WC, Hunt JH, Lyons WG (1997) Life history of the spotted spiny lobster, *Panulirus guttatus*, an obligate reef-dweller. *Marine and Freshwater Research* 48: 687-698

Sheehy MRJ (1990) Potential of morphological lipofuscin age-pigment as an index of crustacean age. *Marine Biology* 107: 439

Skewes TD, Pitcher CR, Dennis DM (1997) Growth of ornate rock lobsters, *Panulirus ornatus*, in Torres Strait, Australia. *Marine and Freshwater Research* 48: 497-501

Smith KN, Herrnkind WF (1992) Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. *Journal of Experimental Marine Biology and Ecology* 157: 3-18

Stonehouse B (1978) *Animal Marking*. Macmillan Press, London

Tarrant MA, Manfredo MJ (1993) Digit preference, recall bias, and non-response bias in self reports of angling participation. *Leisure Sciences* 15: 231-238

Tegner MJ, Dayton PK (1981) Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Marine Ecology Progress Series* 5: 255-268

Trendall J, Bell S (1989) Variable patterns of den habitation by the ornate rock lobster, *Panulirus ornatus*, in the Torres Strait. *Bulletin of Marine Science* 45: 564-573

Uglem I, Noess H, Farestveit E, Jorstad EK (1996) Tagging of juvenile lobsters (*Homarus gammarus* (L.)) with visible implant fluorescent elastomer tags. *Aquaculture Engineering* 15: 499-501

Vannini M, Gherardi F (1981) Dominance and individual recognition in *Potomon fluviatile* (Decapoda, Brachyura): Possible role of visual cues. *Marine Behaviour and Physiology* 8: 13-20

Vianna ML (1986) On the ecology and intraspecific variation in the spiny lobster *Panulirus echinatus* Smith, 1869, (Decapoda, Palinuridae) from Brazil. *Crustaceana* 51: 25-37

von Bertalanffy L (1938) A quantitative theory of organic growth. *Human Biology* 10: 181-213

Wahle RA, Fogarty MJ (2006) Growth and development: understanding and modelling growth variability in lobsters. In: Phillips BF (ed) *Lobsters: Biology, Management, Aquaculture and Fisheries*. Blackwell Publishing, Oxford, pp 1-44

Walters CJ, Martell SJD (2004) *Fisheries Ecology and Management*. Princeton University Press, Princeton

Whiteley DAA, Owen DF, Smith DAS (1997) Massive polymorphism and natural selection in *Donacilla cornea* (Bivalvia: Mesodesmatidae). *Biological Journal of the Linnean Society* 62: 475-494

Williams LE (2002) *Queensland's Fisheries Resources: Current Condition and Recent Trends 1988-2000*. Department of Primary Industries, Brisbane

Wolanski E, Jones M (1981) Physical properties of Great Barrier Reef lagoon waters near Townsville: effects of Burdekin River floods. *Australian Journal of Marine and Freshwater Research* 32: 305-319

Woods CMC, James PJ (2003) Evaluation of visible implant fluorescent elastomer (VIE) as a tagging technique for spiny lobsters (*Jasus edwardsii*). *Marine and Freshwater Research* 54: 853-858

Wydoski R, Emery L (1983) Tagging and marking. In: Nielsen LA, Johnson DL (eds) *Fisheries Techniques*. American Fisheries Society, Bethesda, U.S.A., pp 215-237

Yoshimura T, Yamakawa H (1988) Microhabitat and behavior of settled pueruli and juveniles of the Japanese spiny lobster *Panulirus japonicus* at Kominato, Japan. *Journal of Crustacean Biology* 8: 524-531

Zar JH (1999) *Biostatistical Analysis*. Prentice-Hall, London

Zimmer-Faust RK, Spanier E (1987) Gregariousness and sociality in spiny lobsters: implications for den habitation. *Journal of Experimental Marine Biology and Ecology* 105: 57-71

Zimmer-Faust RK, Tyre JE, Case JF (1985) Chemical attraction causing aggregation in the spiny lobster, *Panulirus interruptus* (Randall), and its probable ecological significance. *Biological Bulletin* (Woods Hole) 169: 106-118

APPENDIX 1

Jolly-Seber Formulae (adapted from Krebs 1999)

The proportion of marked animals (just prior to each census) is given by:

$\alpha_t = (m_t + 1) / (n_t + 1)$

where m_t is the number of recaptured animals at time t, n_t is the total number of animals caught at time t, and the '+ 1' is a correction for bias in small samples (Seber 1973). The size of the marked population (just prior to each census) is given by:

$$M_t = \frac{(s_t + 1)Z_t}{(R_t + 1)} + m_t$$

where s_t is the total number of animals released at time t, Z_t is the number of animals that missed getting caught at time t, but survived and were recaptured later, and R_t is the number of s_t animals caught again after time t. The population size (just prior to each census) is then calculated as:

$N_t = M_t / \alpha_t$

Also, the finite survival rate from time t to time $t + 1$ is given by:

$\Phi_t = M_{t+1} / (M_t + s_t - m_t)$

and the number of individuals joining the population (*i.e.* recruitment plus immigration) between time t and time $t + 1$ is given by:

$B_t = N_{t+1} - \Phi_t(N_t - n_t - s_t)$

Finite (%) and instantaneous (yr^{-1}) rates of mortality are inter-converted as follows:

Finite mortality rate $= 1 - e^{\text{instantaneous mortality rate}}$

APPENDIX 2

Author’s publication list

Frisch AJ (2008) Social organisation and den utilisation of painted spiny lobster (*Panulirus versicolor*) on a coral reef at Northwest Island, Australia. *Marine and Freshwater Research* (In press; accepted 24-9-2007)

Frisch AJ, Baker R, Hobbs J-PA, Nankervis L (2008) A quantitative comparison of recreational spearfishing and linefishing on the Great Barrier Reef: implications for management of multi-sector coral reef fisheries. *Coral Reefs* 27: 85-95

Frisch AJ, Walker SPW, McCormick MI, Solomon-Lane TK (2007) Regulation of protogynous sex-change by competition between corticosteroids and androgens: an experimental test using sandperch, *Parapercis cylindrica*. *Hormones and Behavior* 52: 540-545

Frisch AJ, Hobbs J-PA (2007) Photographic identification based on unique, polymorphic colour patterns: a novel method for tracking a marine crustacean. *Journal of Experimental Marine Biology and Ecology* 351: 294-299

Frisch AJ (2007) Short- and long-term movements of painted lobster (*Panulirus versicolor*) on a coral reef at Northwest Island, Australia. *Coral Reefs* 26: 311-317

Frisch AJ (2007) Growth and reproduction of the painted spiny lobster (*Panulirus versicolor*) on the Great Barrier Reef, Australia. *Fisheries Research* 85: 61-67

Frisch AJ, Ulstrup KE, Hobbs J-PA (2007) The effects of clove oil on coral: an experimental evaluation using *Pocillopora damicornis* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 345: 101-109

Frisch AJ, McCormick MI, Pankhurst NW (2007) Reproductive periodicity and steroid hormone profiles in the sex-changing coral-reef fish, *Plectropomus leopardus*. *Coral Reefs* 26: 189-197

Frisch AJ, Hobbs J-PA (2007) *In vitro* hybridization of coral trouts, *Plectropomus leopardus* (Lacepede, 1802) and *Plectropomus maculatus* (Bloch, 1790): a preliminary investigation. *Aquaculture Research* 38: 215-218

Hobbs J-PA, **Frisch AJ**, Hender J, Gilligan JJ (2007) Long-distance oceanic movement, habitat use and behaviour of a solitary dugong (*Dugong dugon*) at the Cocos (Keeling) Islands. *Aquatic Mammals* 33: 175-178

Hobbs J-PA, **Frisch AJ**, Hender J, Gilligan JJ (2007) New records of Angelfishes (Pomacanthidae) and Butterflyfishes (Chaetodontidae) from Christmas and Cocos (Keeling) Islands, Indian Ocean. *Journal of the Royal Society of Western Australia* 90: 107-109

Frisch AJ, Hobbs J-PA (2006) Long-term retention of internal elastomer tags in a wild population of painted crayfish (*Panulirus versicolor* [Latreille]) on the Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 339: 104-110

Frisch AJ, van Herwerden L (2006) Field and experimental studies of hybridization between coral trouts, *Plectropomus leopardus* and *Plectropomus maculatus* (Serranidae), on the Great Barrier Reef, Australia. *Journal of Fish Biology* 68: 1013-1025

Frisch AJ (2006) Are juvenile coral trouts (*Plectropomus*) mimics of poisonous pufferfishes (*Canthigaster*) on coral reefs? *Marine Ecology* 27: 247-252

van Herwerden L, Choat JH, Dudgeon C, Newman S, **Frisch AJ**, van Oppen M (2006) Contrasting patterns of genetic structure in two species of the coral trout *Plectropomus* (Serranidae) from east and west Australia: introgressive hybridization or ancestral polymorphisms. *Molecular Phylogenetics and Evolution* 41: 420-435

Frisch AJ, Anderson TA (2005) Physiological stress responses of two species of coral trout (*Plectropomus leopardus* and *Plectropomus maculatus*). *Comparative Biochemistry and Physiology* 140(A): 317-327

Frisch AJ (2005) Bachelors seek house and harem: a new tagging technique reveals the cryptic world of crayfish on coral reefs. *Australasian Science* 26: 41-42

Frisch AJ (2004) Sex-change and gonadal steroids in sequentially hermaphroditic teleost fish. *Reviews in Fish Biology and Fisheries* 14: 481-499

Frisch AJ, Anderson TA (2000) The response of coral trout (*Plectropomus leopardus*) to capture, handling and transport stress. *Fish Physiology and Biochemistry* 23: 13-34